

COMPENSATION IN FISH POPULATIONS SUBJECT TO CATASTROPHIC IMPACT

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Under Contract to the
Electric Power Research Institute
Palo Alto, California

Special Report No. 117
Great Lakes Research Division
The University of Michigan
Ann Arbor, Michigan

1985

ACKNOWLEDGMENTS

We wish to thank several people for their contributions to this report. Steven L. Kohler wrote the first draft of the definition of compensation and mechanisms, and wrote part of the annotated bibliography. Philip Hirt and Mary Sweeney rendered valuable assistance by, respectively, conducting much of the literature search and entering text; both made many trips to the library for us. Peter Gable drafted Figure 1.

We thank John Forney, Bernard Skud, Jim Diana, John Palmer, and Jack Mattice for their reviews of the draft; the first two in particular contributed many useful critical comments. Henry Regier and Paul Rago provided several thought-provoking ideas in the early stages of our work. John Blake, as technical advisor, guided us by questions and reminders concerning the direction and focus of the product. We had many stimulating discussions with Robert Otto about our methods of literature search, and how to maximize success of our report and make it most useful to EPRI and to other researchers. Several researchers and biologists were particularly cooperative in providing or discussing unpublished data: Robert Siler, Duke Power Company, Huntersville, NC; Richard McLean, Oak Ridge National Laboratory, TN; Dave Thomas, Charles Main Inc., Boston, MA; David Michaud, Wisconsin Electric Power Company, Milwaukee, WI; and Burt Johansen, Public Service Electric and Gas Company, NJ.

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INTRODUCTION

PURPOSE AND OBJECTIVES

Our primary purposes in this study were to review literature, critically evaluating case histories, to determine the mechanisms and extent of compensation by various fish species subject to catastrophic impacts, and make recommendations for future research. We searched for patterns and relationships among fish species and the compensatory mechanisms they exhibited, with the objective of functionally grouping species. By grouping species, the results could be applied to fish populations for which no data are available. There are relatively few studies where mass fish mortalities have been followed by documentation of subsequent compensation. Thus, we sometimes pieced together evidence of compensation by comparing impacted populations with stable populations elsewhere. To gain a complete picture of compensation by the species we investigated, it was necessary to include data from chronically exploited or impacted populations as well as those catastrophically impacted.

An outgrowth of our literature review was the identification of data gaps. Researchers presented with an impacted fish population or a mass mortality have chosen different ways of documenting it: counting dead fish, tracking the subsequent increase in numbers or biomass, recording growth rates, or sometimes recording fecundity or age-at-maturity changes. Some potential compensatory mechanisms which are difficult to quantify, such as age-specific survival or competition, have been ignored or merely stated as the probable reasons for increased abundance or growth rates. Thus, the full spectrum of potential compensatory response is not known for most fish populations, and many data gaps were identified. Our final objective, then, was to consider the importance and difficulty of obtaining information on previously unquantified compensatory mechanisms and to recommend subjects for further study.

DEFINITION OF COMPENSATION AND MECHANISMS

Introduction

In simplest terms, compensation is any process which leads to a population increasing when at low densities and decreasing when at high densities. There are several levels of organization at which compensation can be considered: ecosystem, community, species, population. Data are usually insufficient to separate stocks, or to ascertain the limits of one population. Therefore, most of our discussion involves a species and assumes the data refer to one integrated population. Although we emphasize compensation at the population level, we include both internal and external mechanisms at that level of organization. Where possible, distinctions are drawn between immigration from neighboring populations and within-population compensation, i.e., increased survival. Immigration presents a problem in analysis for oceans or rivers, where a localized catastrophe usually results in fish moving

in from neighboring areas, not compensation by survivors. The best demonstrations of compensation occur when the entire species undergoes a catastrophic mortality in a bounded system such as a lake.

Population Regulation and Compensation

Many processes can affect the size of populations. Some factors, such as weather and environmental disturbances (e.g., earthquakes, volcanoes) typically affect population size in a density-independent manner. That is, the proportion of individuals affected does not vary with population size. Other processes affect population size in a density-dependent manner (i.e., the proportion of individuals affected varies with population density). Although both density-independent and density-dependent mechanisms may act to influence population size at any point in time or over some time frame, it is generally agreed that density-dependent processes must operate for a population to maintain some long-term "equilibrium" density (Ricklefs 1983).

Density-dependent processes affecting population size can be compensatory or depensatory. Compensatory mechanisms cause an increase in death rate and/or a decrease in birth rate as population size increases and a decrease in death rate and/or increase in birth rate as population size decreases. Depensatory processes tend to decrease birth rate and/or increase death rate as population size declines. Obviously, if only depensatory mechanisms were operating in a population, the population would eventually go extinct. Compensatory mechanisms must operate for a population to have long-term stability. The regulation of fish population size by compensatory processes has received considerable theoretical speculation but relatively little empirical study. The following discussion of compensatory mechanisms is based on reviews by Solomon (1949), Ricker (1954), Cushing (1974, 1977), Gulland (1977), Jensen (1981) and, with particular emphasis on responses of populations to perturbations, by McFadden (1977) and Goodyear (1980). In the following section we will briefly describe the compensatory mechanisms that are thought to be most important in affecting the size of fish populations. Some mechanisms may operate throughout a fish's life cycle (survival, growth) while others primarily operate at a certain stage (Fig. 1).

In general, the process that forms the underlying foundation for the operation of most compensatory mechanisms is how per capita resource availability changes with population density. Food and space (e.g., spawning sites, feeding territories) are frequently cited as resources that can limit fish population size. In the following discussion, we will be concerned with how changes in resource availability affect processes (compensatory mechanisms) which, in turn, affect population size.

Compensatory Mechanisms

Age-specific Fecundity--

Per capita food availability increases as population density declines. This leads to increases in individual growth rates and causes individuals at a given age to be larger than they would be if food was in shorter supply. As

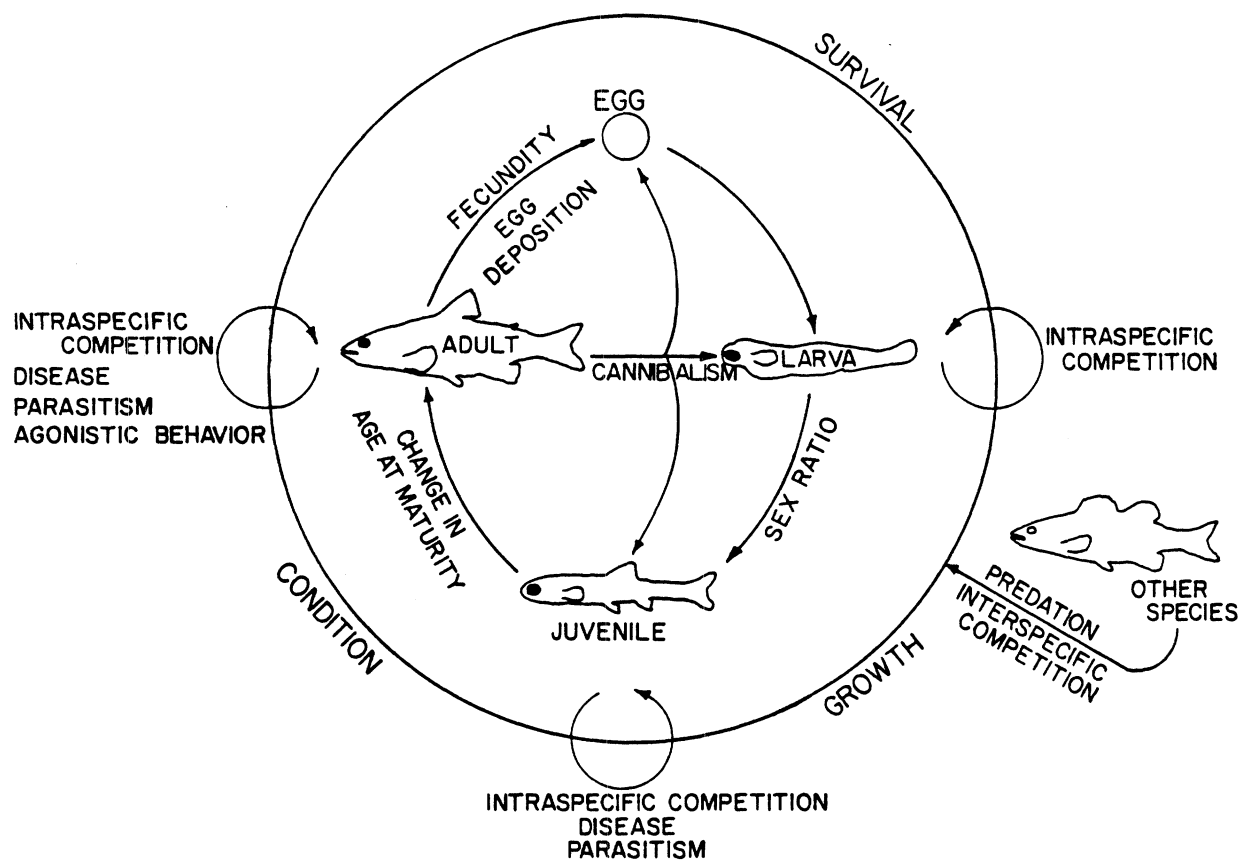


FIG. 1. Scheme of the life history of a fish, showing when various compensatory mechanisms are most likely to operate.

size and fecundity are positively correlated in fish, this leads to an increase in egg production per female as population size decreases (Goodyear 1980; Jensen 1981), which can affect the balance between birth and death rates in a compensatory fashion. For most fishes, the density-dependence of growth declines with age, so for those species, density-dependent fecundity cannot control populations in itself over wide variations in density (Cushing 1977).

Age at Maturity--

This is a related mechanism which operates by influencing the total number of eggs produced per female per lifetime rather than the number of eggs produced per female per reproductive bout. More rapidly growing fish often mature earlier than slower growing fish (with the differences in growth rates resulting from differences in resource availability). Females that mature earlier can produce more eggs in an average lifetime than females that mature later, which leads to an increase in birth rate as population size declines

(Goodyear 1980; Jensen 1981). Earlier reproduction contributes more to "r", the intrinsic rate of increase, than does an equal amount of offspring produced later in life (Birch 1948).

Size-specific Fecundity--

Reduced food availability can affect the number of eggs produced per female independent of any effects of ration on growth rate. A decline in daily ration with increasing population size can reduce the energy available per female for egg production (Goodyear 1980). While this mechanism may be important in growing populations, it is likely of less importance in declining populations since, at a given size, there are physical limitations on the number of eggs that can be produced.

Sex Ratio--

Reduced density may cause more females than males to be produced in the population, or high density may cause more males, as sex is determined phenotypically in at least some fishes (Brown 1970; Torblaa and Westman 1980). Exactly how density determines sex differentiation is unknown. Torblaa and Westman (1980) speculated that high density could induce stress through crowding, influencing differentiation toward maleness; or, that crowding could cause disproportionate female mortality after differentiation. Changes in age composition, growth, and abundance were concurrent with sex ratio changes in Lake Michigan bloaters, *Coregonus hoyi* (Brown 1970). Rapid growth could trigger mechanisms that produce more female offspring (Jensen 1981).

Multiple Spawning During One Year--

This mechanism, though not well documented, may be a compensatory response to low densities for some fish. Egg diameter frequencies and presence of fish larvae in late summer after a catastrophic mortality appeared to indicate that threadfin shad (*Dorosoma petenense*) sometimes spawn twice in 1 year (Kilambi and Baglin 1969; Johnson 1971). The second seasonal complement of eggs may be resorbed at higher fish densities (Johnson 1971). Multiple spawns are, of course, less likely in temperate latitudes than in warmer climates.

Egg Deposition--

In the preceding mechanisms, the total number of eggs produced in the population was affected by population size. It is also possible for population density to affect the number of eggs actually spawned independent of the number of eggs produced. Spawning may be suppressed at high population densities (i.e., some females may not spawn at all - Jensen 1981) due to competition for spawning sites (e.g., salmon - Larkin 1977) or by the excretion of hormone-like repressive factors by members of the population (Goodyear 1980).

Change in Size of Spawning Area--

Pacific sardines (*Sardinops sagax*) and northern anchovies (*Engraulis mordax*) distribute their eggs over a large area at times of high population abundance, then contract their spawning area toward more productive nearshore sites when abundance is low. As a result, at low population levels fish larvae are more concentrated inshore where a high density of food is most likely. Although this maximizes the probability of spawning success, it also increases variability in year-class strength. Conversely, large populations achieve good survival for a part of their range by spawning over a large area, and year-class strength varies less (Radovich 1979).

All of the mechanisms considered above concern means of increasing birth rate as population size declines and vice versa. The remaining mechanisms that will be discussed affect mortality rate in a density-dependent manner.

Predation--

There are two general ways that predation can result in density-dependent mortality in a population. One way results from an interaction between density-dependent growth and size-selective predation. When growth rate is density-dependent, it takes members of a cohort longer to reach a given size as population size increases. If a population exhibiting density-dependent growth is subject to size-selective predation, individuals will be subject to predation longer at high population densities than at low densities. This produces density-dependent mortality since the proportion of the initial cohort size that is eaten increases as the duration of exposure to predation increases (Goodyear 1980). Predation is usually a more important controlling mechanism in early life than later, because as a fish grows its potential predators become less numerous (Cushing 1977). To demonstrate that this mechanism is operating in a population requires that both density-dependent growth and size-selective predation be shown to occur. Note that this mechanism does not require that the predator exhibit a positive numerical response to the density of its prey.

The second general predation mechanism does require the predator to show a numerical response to prey density or a change in feeding behavior with changes in prey density to result in compensatory mortality. If the predator: (1) aggregates in areas of high prey density, (2) feeds more selectively on the prey species as prey density increases, or (3) increases in abundance as prey density increases, the proportion of the prey population eaten may increase as its population density increases (Goodyear 1980).

Cannibalism--

Cannibalism may be an important compensatory mechanism among piscivorous fishes and may be considered as a special case of predation. In populations where age-1 and older fish prey on young of the year (YOY), abundance of age-1 and older fish can strongly affect year-class strength, providing an effective means of regulating population size (Goodyear 1980).

Disease, Parasitism--

These mechanisms operate in similar ways, and show similarities to predation. At high population densities, transmission of bacteria, viruses, or parasites throughout the population is more likely to occur than at low densities, if high densities increase the number of intraspecific contacts. As high populations deplete food supply, increased food-seeking movements coupled with decreased resistance would promote the spread of disease organisms (Solomon 1949). The disease organisms, parasites, and predators whose density-dependent action is most pronounced are those which concentrate on one species for prey or host. Parasites, diseases, or predators may be reduced greatly when the host or prey population is at low density, so that the host can increase again for a time before control is again exerted (Solomon 1949).

Incubation Mortality--

Eggs may survive better at low densities than at high densities. Oxygen demand may be limiting at high egg densities (Johnson 1965), and waste product buildup may reach toxic proportions (Hunter 1959; Foerster 1968). Closely spaced eggs are also more prone to fungal infection (LeCren 1965).

Interference Competition; Agonistic Behavior--

Aggressive competition for feeding territories can lead to compensatory mortality. Individuals of species that are territorial and are unable to establish territories may be more susceptible to starvation or predation than individuals that successfully establish territories. If space for feeding territories is limiting, the proportion of individuals using less favorable territories, or unable to establish territories at all, will increase as initial population size increases and, consequently, the mortality rate will increase as population size increases (Goodyear 1980).

Starvation--

Mortality resulting from starvation in early life history stages is considered to be a potential, though not well documented, means of population regulation. Starvation mortality can be compensatory only if the population, and not some other factor, is responsible for reducing its food supply (Goodyear 1980). Starvation is believed to be most important just after yolk-sac absorption, termed the "critical period" (Hjort 1914), but may occur at other life stages as well. While food may be limited and reduced by the population, many fish do not actually die from lack of food but are weakened, so that they are more vulnerable to other causes of mortality.

Mortality Resulting from Stress--

In many populations, the probability of an individual surviving stressful conditions (e.g., overwintering conditions) increases as individual size increases. Consequently, if growth rates of individuals in the population are density-dependent, the proportion of individuals that survive stressful conditions increases as population size decreases (Goodyear 1980).

Rosenthal and Alderdice (1976) discussed the effect of sub-lethal stressors on marine eggs and fish larvae. They said that it was important to identify stressors but it was more complex to identify the consequences and ecological implications to fish. Temperature and salinity affect the size of Pacific herring (*Clupea harengus pallasii*); no jaws develop at $< 5^{\circ}\text{C}$. Radiation causes eye malformations, and cadmium causes the death of eggs. Studies provide insight and recognition of basic pathways a fish may follow to compensate for environmental stress. The scope for compensation is limited in the basic mechanisms involved and changes as development proceeds from the egg onward. The basic reaction to chemical insult at the egg stage occurs at the biochemical level--decoupling of oxidative phosphorylation and blocking production of ATP. This can cause the dedifferentiation of cells and retard development of eggs. Low temperature and low dissolved oxygen can cause stress and lengthen the time to hatching. DDT exposure causes weaker swimming which can affect food gathering and the ability to escape predators. Exposure to pollutants can cause difficulty in maintaining position in the water column, causing decreased feeding and increased predation. Many effects channel back to a few compensatory responses. Most sub-lethal effects are biochemical. Fish appear to trade certainty of death at one stage for decreased survival at the next.

Integrative Mechanisms--

Growth and condition factor are two easily measured parameters which relate to several of the aforementioned compensatory mechanisms. Increases in growth rate or condition are taken as evidence that compensation is occurring - evidence that decreases in competition had permitted increased growth, and greater size-at-age would then increase fecundity or decrease predation, cannibalism, mortality from stress, or age at maturity. Because competition, predation, cannibalism, and stress mortality are difficult to quantify, density-dependent growth in length or weight is often treated (in the literature and in this report) as a compensatory mechanism in itself.

Density-dependent survival is a general term for a compensatory process consisting of several potential mechanisms: predation, cannibalism, disease, parasitism, starvation, and stress mortality. Similar to the growth rate-condition factor situation, survival is sometimes treated as one compensatory mechanism because its components may be very difficult to separate or measure. Many fish populations are believed to be stabilized by density-dependent mortality before recruitment (Cushing 1977).

General Concepts of Compensatory Response

Compensatory processes and population regulation differ when a community or an interacting system of stocks or subspecies, rather than one population, is involved. One species may compensate better than, or instead of, another species. A different set of processes may control populations after a perturbation than controlled them before (Goodyear 1980), which is sometimes due to community changes, sometimes environmental changes. The new processes prevent an impacted population from recovering its former level of abundance and cause it to be stable at a new decreased level. Holling (1973) termed such discrete equilibria "domains of attraction." He cited the example of Great Lakes fisheries: a period of intense exploitation with high harvests followed by a sudden, precipitous drop in populations. Although fishing pressure was then relaxed, populations did not recover to former levels of abundance; this was not entirely attributable to environmental change (Holling 1973). Thus, it is apparent that extent and mechanisms of compensation after catastrophic impacts may not be of the same order as compensation for a chronically exploited species. Failures to recover from impact are part of our results and help determine the limits of compensatory reserve.

Compensatory reserve is defined quite precisely by Goodyear (1977) as the difference between a stock's existing compensation ratio (which is related to fecundity and survival of exploited and unexploited populations) and the critical limit of the compensation ratio beyond which the population tends toward extinction. Compensatory reserve is related to resiliency of a population, its ability to withstand additional stress. Resilience is decreased by added mortality, making a stock more vulnerable to chance destruction by environmental change or fluctuations in mortality factors already present (Ricker 1977; Goodyear 1980). Evidence of compensation (e.g., high growth rates or fecundity) may therefore indicate a population with already-reduced resilience (the cause may be unknown), so that a higher exploitation rate is unwise. More complex systems, those with greater numbers of species, tend to have less variable, more resilient populations (Solomon 1949). Holling (1973) uses resilience in a broader sense: "a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables." Holling also defines stability as the ability of a system to return to equilibrium after a disturbance. Under these definitions, a highly unstable system, one which fluctuates widely between domains of attraction, would also be resilient if it always maintains the same relationships (e.g., spruce budworm forest community). Great Lakes fisheries provide an example of stable but non-resilient systems (Holling 1973). In our report, we will use the narrower definition of resilience as the ability of a population to withstand stress without catastrophic collapse.

CATASTROPHIC IMPACT

For the purposes of this investigation, we defined a catastrophic impact as an event which removes some limitation(s) on a fish population, such as food or space. Thus we included new species introductions, as well as mass

fish mortalities, as examples of catastrophes. (The catastrophic event as defined here applies only to the species introduced, not to other species already present in the system.) In either case, resources are suddenly relatively more abundant than before, or species may be released from competitive or predatory pressure. In some instances, introductions illustrate species expanding numerically when they fill a "vacant niche," or take advantage of an unused food resource, exemplifying compensatory ability after a short-term event.

Catastrophic events have various means of impacting fish populations (Table 1). These events may kill only a particular age-group; e.g., drawdown may kill demersal eggs or relatively immobile larvae inhabiting shallow water, while catastrophic overfishing removes adult fish. Such changes in the age structure of the population have implications for its potential compensatory response. Similarly, events with lingering effects such as toxic spills, where the substance may remain in the system for years before decomposing or flushing out, may inhibit or prevent a compensatory response. Other species may take advantage of an impact to one species, and compensate at the expense of the impacted species. Thus changes in community composition, or a different domain of stability (Holling 1973; Goodyear 1980), may result from a catastrophic impact. These implications will be considered in species accounts and applied to groups of species in our discussion.

Catastrophe theory (Zeeman 1976; Jones and Walters 1976; Walters et al. 1980) offers a concept to understand relationships between fish stocks and their controlling factors. Exploited fish populations may be operating close to a "cliff edge" so that slight increases in fishing mortality or natural mortality such as predation would cause a stock collapse. This has occurred in the Atlantic herring (*Clupea harengus harengus*) fishery. The catastrophe theory concept was developed by Walters et al. (1980) for lake trout (*Salvelinus namaycush*). Fishing and sea lamprey (*Petromyzon marinus*) predation decrease the domain of stability of spawner biomass; i.e., the upper equilibrium biomass moves closer to the lower critical biomass. When these biomasses reach the same level, the stock collapses. With decreased fishing effort, lamprey control, and some stocking, the fishery recovered, as predicted by the model.

Catastrophe theory is consistent with the existence of critical depensation, where an infinitesimal increase in fishing effort leads to an unstable state followed by extinction. This would result when mortality increases as stock levels decline (which may be true for schooling fishes) so that a depensatory relationship exists between stock and recruitment at low stock levels (Clark 1974). When fishing has caused a population to lose its resilience (Holling 1973), random fluctuations in reproductive success or in the environment may precipitate a stock collapse (Clark 1974). Critical depensation would also occur when factors that are normally density-dependent (e.g., predation, parasitism) begin to act more intensely as the subject population decreases and cause a catastrophic decline. An example is the predicted collapse of Lake Michigan alewives (*Alosa pseudoharengus*) due to continued stocking of salmonid predators (Stewart et al. 1981), which continued targeting alewives even when alewife populations began to decline

TABLE 1. Characteristics of some catastrophic impacts. See Table 3 for published studies which are examples of catastrophic impacts followed by compensation.

Category and catastrophe	Subject of catastrophe (fish, habitat)	Cause	Fish life stage impacted	Other species affected?	Lingering effects
Experimental Drawdown	habitat	man	young	yes	affects plant communities
Pond manipulations	either	man	any	possibly	?
Toxicant treatments	fish	man	any	yes	some toxicants, yes
Toxic spill	both	man	any	yes	yes
Species introductions	fish	man	any	yes	yes
Weather-related catastrophes: (winterkill, storms, upwellings, abrupt temperature changes, drought, red tide, estuary salt & freshwater mixing, El Nino)	usually fish	natural	any	yes	no

TABLE 1. Continued.

Category and catastrophe	Subject of catastrophe (fish, habitat)	Cause	Fish life stage impacted	Other species affected?	Lingering effects
Overfishing leading to population collapse	fish	man	adults	usually no	usually not, if fishing stopped or much reduced
Density-dependent agents acting in compensatory way					
Disease	fish	natural	any	usually no	maybe (decreased health of fish)
Competition	fish	natural	any	yes	maybe (domain of stability)
Predation	fish	natural	especially young	yes	maybe (domain of stability)
Parasitism	fish	natural	especially adults	usually no	maybe (decreased health of fish)

(J. F. Kitchell, University of Wisconsin - Madison, personal communication; Great Lakes Research Division unpublished data). Other catastrophic impacts, such as experimental manipulations, toxic spills, and species introductions, are generally not described by catastrophe theory because these events are not a continual part of the system (as fishing or predation are), and their "big effects" are from big causes, not small causes as expressed by Ricker (1963); there is no discontinuity or "cliff edge" in the behavior of the system. Predation, overfishing, competition, disease, and parasitism are all potential catastrophes which, however, usually do not cause a catastrophic impact; when they do, it is a special case.

METHODS

LITERATURE SEARCH

We began our search of the primary literature by examining recent (1979-1984) abstract listings and indexes: Biological Abstracts, Sport Fisheries Abstracts, Current References in Fish Research (Cvancara), and Science Citation Index. The most productive subject keywords included population studies, mortality, introductions, species names, and causes of mass mortalities such as toxicity, winterkill, and pond experiments. Several useful papers were found in "Compensation in Fish Populations: A Partial Bibliography" compiled by T. Gregory of Science Applications, Incorporated. Many compensation-related studies were discovered in literature cited sections of reference works and classic studies. The most fruitful of these were Ricker (1954), Beverton and Holt (1957), Gerking (1967), LeCren et al. (1977), Gulland (1977), McFadden (1977), Clepper (1979), and Goodyear (1980).

Science Applications, Incorporated, conducted a computer search for us using keywords we supplied (Table 2). This search resulted in a list of 139 papers, about 20 of which were pertinent to our subject. We checked literature cited sections from all papers obtained from all of the above sources, resulting in a branching network of literature. Approximately 800 papers were viewed from the primary literature, about 300 of which proved to be useful for this project.

Gray literature was investigated primarily through personal contacts. We spoke to industry, academic, and research biologists in attempts to obtain unpublished data and learn of obscure studies. Many data sets exist which could complement published studies or stand alone in demonstrating compensation; however, many are not summarized and are in too raw a form for us to use them given our limited time and resources. Any such data sets we discovered are mentioned in species accounts for future reference.

We visited the libraries of two government agencies in our area, the Great Lakes Fishery Laboratory of U.S. Fish and Wildlife Service and the Institute for Fisheries Research of the Michigan Department of Natural Resources, in an effort to obtain unpublished studies.

ORGANIZATION OF RESULTS

One of the results of this project was the annotated bibliography, Appendix 1. Selected papers were critically reviewed for appropriate methods (sampling gear, experimental design, data analysis) and applicability of the data to compensation studies. For each entry, the bibliography includes the citation, keywords, abstract, selected data, and our review. Keywords were selected to facilitate use with an editing computer program so papers on a particular subject could be retrieved. Keywords included fish species, geographic region, type of catastrophic event, and compensation mechanism(s).

TABLE 2. Keywords used for computer search done by Science Applications, Incorporated.

All combinations of these	With these
fish kills	compensation
toxic spills	compensatory growth
winterkill	compensatory mortality
storms	compensatory survival
temperature or thermal shock	density-dependent growth
catastrophe	density-dependent mortality
population collapse	density-dependent survival
overfishing	fecundity
die-off	sex ratio
competitive interference	sexual maturity
drawdown	carrying capacity
experimental fish kills	abundance
fish toxicants	growth
drought	mortality
red tide	survival
El Nino	cannibalism
salinity change	condition factor
disease	disease
predation	predation
parasitism	parasitism
competition	competition

Any literature useful for quantifying compensation after a catastrophe was read and assimilated. Table 3 presents all studies used in this report where catastrophes were followed by data documenting compensation. For this report, a number of separate species accounts were written (see CASE HISTORIES), although some species were grouped. Species are addressed in taxonomic order. Examples of catastrophic mortalities are summarized. Compensatory mechanisms are listed and, whenever possible, quantified. Cases where populations were decreased beyond their ability to recover were also included to demonstrate the limits of compensation. We have reported extreme values of growth, fecundity, and some other life history parameters, as such values may reflect compensatory responses. Given that a species exhibits a compensatory response, a catastrophe that drastically lowers population density probably induces a greater response than a small impact; thus extreme values may result from extreme impact. The literature often demonstrates the operation of compensatory mechanisms which are difficult to quantify or not measured for the species in question - competition, predation, cannibalism on larvae, stress mortality, early survival. We report these qualitatively when no quantitative data are available.

The SYNTHESIS section includes an overview of the results, discussion of studies on other species, and general topics. We looked for patterns in compensatory responses in an attempt to functionally group species, to make generalizations and predictions about species for which data are not available. Summaries of data gaps are deferred to the SYNTHESIS section.

TABLE 3. Published studies of catastrophic mortalities to fish populations with information on subsequent compensation used in this report.

Category and catastrophe	Author(s) and date	Species
<u>Experimental</u>		
Drawdown	Johnson 1970, 1971	Threadfin shad
Pond or lake manipulations, experimental fishing	Bagenal 1977	Eurasian perch, northern pike
	Healey 1980	Lake whitefish
	Johnson 1977	Yellow perch, walleye, white sucker
	Lawler 1965	Yellow perch, northern pike
	LeCren et al. 1977	Eurasian perch
	Priegel 1971	Freshwater drum
	Ricker and Gottschalk 1940	Yellow perch, walleye, others
	Rose 1957	Gizzard shad
	Rose and Moen 1952	Yellow perch, walleye, freshwater drum
	Swingle 1949	Gizzard shad
Toxicant treatments	Beckman 1941, 1943	Rock bass
	Grice 1959	Yellow perch, others
	Higley and Bond 1973	Chinook, coho salmon
	Huish 1957	Gizzard shad
	Phillippy 1964	Threadfin shad, gizzard shad
	Torblaa and Westman 1980	Sea lamprey
<u>Toxic spill or acidification</u>	Beamish 1976	Yellow perch
	Ryan and Harvey 1980	Yellow perch
	Svardson 1976	Yellow perch
<u>Species introductions or new impoundment</u>	Alm 1946	Yellow perch
	Bodola 1966	Gizzard shad
	Bryant and Houser 1968	Threadfin shad
	Fraser 1978	Yellow perch
	Jackson 1957	Gizzard shad
	Kilambi and Baglin 1969	Threadfin shad
	Mahon and Ferguson 1981	White sucker, minnows
	Miller 1957	Alewife
	Patriarche and Campbell 1957	Gizzard shad

TABLE 3. Continued.

Category and catastrophe	Author(s) and date	Species
	Smith 1968	Alewife
	Wells 1977	Alewife, yellow perch
<u>Weather-related catastrophes</u>		
Winterkill	Beckman 1950	Bluegill, pumpkinseed, yellow perch
	Bergstedt and O'Gorman 1983	Alewife
	Kohler and Ney 1981	Alewife
	Siler et al. in press	Threadfin shad
Abrupt temperature changes	Brown 1968, 1972	Alewife
	Elrod et al. 1980	Alewife
Storms and floods	Hanson and Waters 1974	Brook trout
Upwellings, drought, red tide, El Nino, estuary salt and freshwater mixing	none	
<u>Overfishing leading to population collapse</u>	Anderson and Smith 1971	Lake herring
	Brown 1970	Bloater
	Parsons 1970	Walleye
<u>Density-dependent agents acting in depensatory way</u>		
Disease	Bardach 1951	Yellow perch
	Craig 1980	Eurasian perch
	Van Oosten 1947	Rainbow smelt
Parasitism	Burrough and Kennedy 1979	Roach
Predation	Forney 1971	Yellow perch
Competition	none	

CASE HISTORIES

INTRODUCTION

We chose to concentrate our efforts on a limited group of fish species in order to maximize our results and be certain of thorough analysis for the species selected. We used several criteria in choosing species: (1) various life history strategies, (2) geographic locations, and (3) taxonomic placements were to be represented (Table 4); and (4) species chosen were those for which information was known to be available, including species already known to exhibit mass mortalities or wide fluctuations in abundance.

TABLE 4. Characteristics of species chosen for this report. F = fish (piscivorous); P = planktivorous; O = other (combination or benthos); r and K = r- and K-selected species.

Species or group	Life history strategies	Food of adults	Geographic location represented in this report	Family
Alewife	r	P	Great Lakes, Virginia	Clupeidae
Threadfin shad	r	P	Southeast, Southwest	Clupeidae
Gizzard shad	r	P	Great Lakes, Southwest, Southeast	Clupeidae
Lake whitefish	K	O	Great Lakes, Canada, far North	Salmonidae
Pacific salmon	K	F	Northwest	Salmonidae
Rainbow smelt	r	O	Great Lakes	Osmeridae
Yellow perch	r	O	Great Lakes, Midwest, New York, England	Percidae
Walleye	K	F	Great Lakes, Midwest, New York, Canada	Percidae
Freshwater drum	r	O	Great Lakes, Midwest, South Central	Sciaenidae

ALEWIFE

Introduction

The alewife (*Alosa pseudoharengus*) is native to Atlantic coastal waters of the United States, but enters fresh water to spawn and has established landlocked populations in several areas. Also, the alewife has been purposely introduced in lakes and reservoirs in order to exploit unoccupied niches as a pelagic planktivore and to provide forage for sport fishes. Alewives inhabiting coastal waters, inland lakes, and the Great Lakes have different

population and growth characteristics, relationships with other species, and vulnerability to mortality factors, all of which may affect compensation by alewife. Catastrophic mortalities have not been documented for coastal populations of alewife. There are four possible reasons: (1) fishing mortality has not been excessive or has been compensated for rapidly, (2) alewives evolved in salt water, so are not subject to osmotic stress there, as opposed to alewives in fresh water, (3) water temperature fluctuations are more common and of greater magnitude in bodies of fresh water than in the sea, and (4) alewives may be more controlled by predation in the sea, leading to better growth and condition. Therefore discussion will focus on freshwater alewife populations and the mass mortalities common to them.

Alewives in Lake Ontario may live up to 10 years (Bergstedt and O'Gorman 1983). Less than 1% of alewives trawled from Lake Michigan in 1964-1970 were more than 6 years old (Brown 1972), although annuli may not form when growth is suppressed (Bergstedt and O'Gorman 1983), so some alewives may be older than their scales indicate. Fecundity in Lake Michigan, 1964-1965, was 11,000 to 22,000 eggs, increasing with length (Norden 1967), but anadromous alewives produce 60,000 to 100,000 eggs per female (Belding 1921 cited in Norden 1967). Survival is only about 1% during the first 3 months after hatching (Mansfield and Jude in press). Freshwater alewives mature at age 1, 2, or 3 in various waters (Nigro 1980). The high fecundity, early maturity, and mortality at early life stages of the alewife imply high potential for increase and high compensatory capability.

Catastrophic Mortalities

Great Lakes--

Alewives became abundant in Lake Ontario in the late 1800s and suffered a number of die-offs from 1876 to 1928 (Pritchard 1929). Although the Welland Canal was completed in 1829, alewife did not colonize the rest of the Great Lakes immediately. In each of the upper four lakes, increases in alewife abundance did not occur until predator abundance declined: for Lake Erie, walleye (*Stizostedion vitreum vitreum*), blue pike (*S. vitreum glaucum*), and sauger (*S. canadense*) declined in the late 1920s; and in the other lakes, lake trout declined in the 1940s and 1950s (Smith 1970). This appears to exemplify compensation after release from predation, but data are insufficient to quantify predation during those years. Supporting the predator-alewife relationship, Lake Michigan alewives have declined in abundance since about 1976. This is probably attributable to continued salmon stocking and apparent preference of salmon for alewife prey, even when other prey are more abundant - a compensatory relationship (Stewart et al. 1981; J. F. Kitchell, University of Wisconsin - Madison, personal communication; Great Lakes Research Division unpublished data). The intrinsic rate of increase for alewife is demonstrated by the explosive increase in Lake Huron populations during the 1950s (Miller 1957) and in Lake Michigan populations during the early 1960s (Smith 1968; Table 5). The increases could have been accomplished through several mechanisms, including increased survival of young alewives, decreased competition, predation or cannibalism, or increased growth, which are all

interrelated. Colonization of Lakes Michigan and Huron by alewife is analogous to a population increase after a catastrophic impact; in both cases, limiting factors are decreased or absent, allowing exponential increase of the population until it approaches carrying capacity. Capacity for alewife in Lake Michigan was reached or exceeded during the mid-1960s, as indicated by an increase in average age of stock between 1965 and 1966, failure of the large 1964 year class to increase adult stocks in 1966 (Smith 1968), slow growth of adults, and the mass mortality in 1967 (Brown 1968, 1972).

Several billion alewives, about 70% of Lake Michigan's population, died in the 1967 mortality (Wells and McLain 1972). Alewives compensated after the mortality by increasing growth in length and weight, and increasing survival, shown by increase in average age (Brown 1972). Growth changes occurred primarily in age-classes 3 through 5, and possibly later. Ages 3 through 5 grew 7.1 to 23.7% faster during 1967 than the 1962-1969 means (Brown 1972). Average weight increased 16-26% immediately after the die-off. Females increased length more than males, but males put on relatively more weight than females (Brown 1972), possibly suggesting that fecundity did not increase greatly. Mean age was 2.6-3.0 yr in 1965-1966, increasing to 3.2-3.8 in 1968-1970, reflecting improved survival (Brown 1972). Ages of these alewives could have been incorrect because suppressed growth in turn may suppress annulus formation (Bergstedt and O'Gorman 1983). Poor condition prior to the die-off, because of high density, caused alewives to be more vulnerable to low-temperature stress, and conversely, improved condition after the die-off increased alewife resistance (Brown 1972). Another example of density-dependence is the apparent inverse relationship between recruitment each year and abundance of adults during fall of previous years; however, variability obscures some of this relationship (Brown 1972). The Wisconsin Department of Natural Resources, Wisconsin Electric Power Company, and U.S. Fish and Wildlife Service have further unpublished data on Lake Michigan alewife populations.

A die-off similar in magnitude to the 1967 Lake Michigan die-off occurred in Lake Ontario during the winter of 1976-1977. As many as 75% of the Lake Ontario alewives died, mostly the youngest age-groups (Elrod et al. 1980). The 1976 year class was virtually eliminated, and a strong year class was produced during 1977. The abundant 1977 year class appeared in 1979 spring trawl catches, where 67% of the alewives were age 2, compared to 7% and 0% in 1972 and 1978 catches respectively. Alewife adults increased sevenfold from 1978 through 1981 (Bergstedt and O'Gorman 1983). Condition factor and growth showed compensation during this period, both being poor the year before the die-off and increasing markedly during 1977, declining again in 1978. During 1977, age-groups 2, 3, and 4 increased in length by increments which were 2-3 times the calculated increments of the previous year (Table 6). Alewife of age-groups 4-6 were generally longer (up to 11 mm) in 1979 than those of the same ages in 1978 because of the large growth increment in 1977. Elrod et al. (1980) had expected a small die-off in spring 1979, but a substantial mortality occurred. They believed the hot, calm weather precipitated the die-off. If so, it is an example of density-independent factors exacerbating mortality and relates to other studies suggesting a combination of density-dependent and density-independent contributions to

TABLE 5. Abundance of alewife in Lake Michigan, 1959-1967. Blank = no data.

Year class	Young of the year abundance index (1962=100) ^a	Age 3 abundance index (1965=100) ^a	Age 0 abundance index ^b	Adult abundance index ^b	Age 0 ^c	Adult ^c	Commercial landings (thousand kg) ^b
1959		23					575
1960		23					1,077
1961		37					1,454
1962	100	100	20	87	31	86	2,155
1963	391	400	78	76	137	82	2,453
1964	4,971	5,000	1,054	144	1,740	151	5,338
1965	3,906	3,900	566	420	1,562	432	6,367
1966			131	439	215	450	13,183
1967			72	234			19,043
1968			946	54			12,361
1969			1,134	146			13,295
1970			790	138			15,210

^a Bureau of Commercial Fisheries unpublished data.

^b Brown (1972).

^c Smith (1968).

catastrophic alewife mortalities. Winter mortalities again increased in 1981-1982, but were small in 1982-1983, which was a very mild winter (Bergstedt and O'Gorman 1983). Unpublished data by the same researchers show record numbers of alewives in Lake Ontario in 1983, followed by a die-off of about 50% that winter, the largest decline since 1977. During fall 1983, adult alewives were in worse condition than they had been in spring, suggesting a die-off was imminent. Alewives 150-179 mm long averaged 29.7 g in fall 1983, compared with 32.5 g in 1982 to spring 1983 and 41.1 g in 1977 (Bergstedt and O'Gorman 1983). In addition, water temperature during mid-April 1984 was the second lowest recorded during 1979-1984. In summary, Lake Ontario alewife data show compensation in growth and condition factor, and probably also survival of early life stages as evidenced by large numbers of age-0 alewives.

Small Freshwater Systems--

Alewives were introduced to Claytor Lake, an impoundment in Virginia, in 1968-1969. Virginia is near the southern edge of the alewife's native coastal range (Scott and Crossman 1973), and this lake contained the first southeastern landlocked population (Kohler 1980). Die-offs occurred regularly during the winter, but were apparently not a large fraction of the population. Growth rates during 1971 were fairly rapid compared with Great Lakes alewife populations (Boaze and Lackey 1974; Table 6). A massive die-off occurred during winter 1977-1978 (Kohler and Ney 1981). Although percent mortality was not estimated, no alewives were collected during intensive sampling in spring 1978 (until mid-June), implying a substantial proportion of the population was lost. Most alewives collected in 1979 were age 1, showing a strong year class was produced despite the reduced stock (Kohler and Ney 1981). Alewife growth, when compared between 1976-1977 and 1978, increased significantly for age-groups 2 and 4. Kohler and Ney (1981) discussed reduced intraspecific competition as the reason for growth compensation and presented zooplankton data as evidence. Alewives selected zooplankters ≥ 1 mm, and large zooplankton species were more abundant in summer 1978, just after the die-off, than in summer 1979 (Kohler 1980). Alewives as small as 35 mm, young of the year, selected large zooplankton (Nigro 1980). These data are similar to results obtained for Lake Michigan by Wells (1970) and for Connecticut lakes by Brooks and Dodson (1965) showing alewives change the size structure of zooplankton populations. Kohler and Ney (1981) did not present condition data, but their results concerning growth and strength of the first year class after catastrophe agreed with results of Great Lakes studies. This study demonstrated the extreme resilience of an alewife population that was drastically reduced.

Causes and Effects of Mortalities--

Proposed contributing factors to mass mortalities of alewife include warm temperatures, cold temperatures, sudden temperature changes, fungus (*Saprolegnia*), iodine deficiency, electrolyte imbalance, and high densities of alewife (Graham 1956; Brown 1968; Smith 1968; Colby 1971, 1973). *Saprolegnia* infected only 20% of alewives sampled during the 1967 die-off, and was not believed to be an important factor (Brown 1968). Christie (1973) stated that

TABLE 6. Growth increments (mm) by age-group for alewives before and after catastrophic mortalities at various locations.

Location, source and time	Age-group				
	0	1	2	3	4
Landlocked, freshwater populations					
Lake Michigan					
Brown (1972) ¹					
1965	97/97	-2.2/-2.3 ²	0/-2.6	-10.3/-15.0	-23.4/-14.5
1966	98/99	2.6/-0.7	3.9/6.2	-10.3/-7.0	-10.4/-10.5
1967	99/100	3.5/1.9	7.1/9.2	9.2/19.0	16.9/23.7
1968	92/94	2.4/4.1	-3.2/-13.8	9.2/18.0	16.9/19.7
1969		-5.9/0.4	-7.7/-16.4	8.0/5.0	0/15.8
Lake Michigan					
Norden (1967) ¹	95	46	19	13	
Lake Ontario					
Elrod et al. (1980)					
1975	91	36	13	9	8
1976	ND	37	13	8	7
1977	91	ND	35	31	28
1978	ND	56	ND	8	11
Lake Ontario					
Graham (1956) ¹	77	57	22	5	23
Claytor Lake, Virginia					
Kohler and Ney (1980) ¹					
1976-1977	163	19	18	7	
1978	160	57	25	19	
Seneca Lake, New York					
Odell (1934) ¹	68	76	7	17	4
Lake Hopatcong, New Jersey					
Gross (1959) ²	76	32	42		

TABLE 6. Continued.

Location, source and time	Age-group				
	0	1	2	3	4
Landlocked, freshwater populations					
Cayuga Lake, New York Rothschild (1965) ²	102	19	9	8	6
Echo Lake, Maine Lackey (1970) ¹	114	61			
Anadromous populations					
Hamilton Reservoir, Rhode Island Richkus (1975)					
1970	106				
1971	91				
1972	102				
Long Pond, Maine Havey (1961)	135	86	53	28	13

¹ Back-calculations from scale analyses.

² Percent deviation of increments from the 1962-1969 means. Male/
Female.

³ Length-frequency analyses.

severity of mortality was probably related to water temperature, and alewife abundance may not necessarily cause die-offs, but die-offs would not be noticeable during periods of low density. Thus alewife die-offs are most likely density-independent, except at periods of such extremely high density that condition factor comes into play. Poor condition results in increased susceptibility to low temperature stress, but cold temperatures alone may cause alewives to stop feeding and die (Colby 1973). Any attempt to predict occurrence and extent of alewife mortalities must consider water temperature, which fluctuates somewhat erratically in the Great Lakes.

Temperature-related mortalities should not affect the subsequent ability of alewives to compensate. Age structures of alewife populations are changed by die-offs. Usually spring and early summer die-offs consist primarily of adult alewives, and fall die-offs are of young-of-the-year or yearling alewives (Pritchard 1929; Graham 1956). This may be explained by the tendency

of age-groups to inhabit different water depths and strata (Wells 1968), becoming exposed to temperature gradients at different times. However, age structure changes should not affect an alewife's ability to compensate, because sexual maturity comes at an early age (males may spawn at age 1 and females at age 2 - Pritchard 1929). Thus even if all alewives age 2 or more died, spawning could occur the following year and the population could recover quickly due to the alewife's great resilience. We did not find a case of mass mortality from which an alewife population did not recover. So far, although Lake Michigan alewife populations are being held low by depensatory salmonid predation, alewife reproduction is still occurring (Great Lakes Research Division unpublished data). Therefore the potential still exists for alewives to rebound in Lake Michigan.

Compensatory Mechanisms

Few compensatory mechanisms have been documented for alewife, although we believe some undocumented mechanisms to be operating. Those that have not been documented are age-specific fecundity, size-specific fecundity, sex ratio, egg deposition, predation, disease, parasitism, and interference competition. Fecundity probably is density-dependent for alewife, because the alewife shows density-dependent growth (although perhaps only under extreme changes) and larger fish have larger gonads, producing more eggs (Norden 1967). However, the only data found for fecundity related to density showed a downward trend in number of eggs per gram body weight for a chronically impacted Lake Michigan population during 1973-1975 (Gerking 1976). There were no data relating fecundity to age. The limited predation data and circumstantial evidence available indicate, for Lake Michigan at least, predation is density-independent or depensatory. Although competition has not been documented or quantified, the changes in Lake Michigan zooplankton and the alewife's density-dependent growth suggest that competition may well be an important regulator and affect survival. Improving early survival is a potent mechanism for quickly increasing abundance, which alewives have been shown to do.

Age at Maturity--

Alewives matured earlier in Claytor Lake (most at age 1) than in Lake Michigan (age 2), probably because of faster growth (Nigro 1980). Therefore, the density-dependent growth usually observed after a mass mortality should result in a lower average age at maturity.

Cannibalism--

Few studies have documented cannibalism by alewife. During 1971 and 1972 in Lake Michigan, alewife larvae were about 20% of the volume of adult alewife stomachs (Rhodes et al. 1974). Alewife abundance was fairly high during those years. In Claytor Lake during the 2 years after the die-off, only 5 out of 524 alewives collected had consumed larval alewives (Kohler and Ney 1980).

Some adult Lake Michigan alewife we examined during fall, 1973-1982, contained alewife larvae >15 mm (Great Lakes Research Division unpublished data). These results represent some slight evidence for density-dependent cannibalism. Since cannibalism is documented for alewife, presumably it would be more frequent at high densities than at low densities, and possibly would be compensatory.

Starvation and Mortality Resulting from Stress--

These two mechanisms work interdependently for alewife, as demonstrated by the Great Lakes case histories. Although actual starving to death is not documented for alewife, density-dependent condition factor implies food limitations. Annual die-offs often correspond with seasonal energy lows (Flath and Diana 1985). A high proportion of alewife mortality in the 1960s was probably due to overwintering and spawning stress combined with insufficient lipid storage (i.e., feeding) in the fall (Flath and Diana 1985), possibly due to intraspecific competition (Brown 1972). The conclusion of most researchers is that poor condition due to limited food makes alewives more vulnerable to low temperature stress, and conversely, alewives grow faster after a mass mortality because of decreased intraspecific competition for food (Brown 1972; Colby 1973; Kohler and Ney 1981; Bergstedt and O'Gorman 1983). This of course is an interpretation of the data, but it appears to fit better than other explanations such as fungus infection or electrolyte imbalance, which may be results of stress rather than causes.

Summary

Landlocked alewife populations are more prone to wide fluctuations and catastrophic mortalities than anadromous populations. After catastrophic mortalities, freshwater alewife populations usually demonstrate improved growth and condition of adults and increased abundance of young. The data and case histories suggest that at low densities, decreased intraspecific competition is the mechanism bringing about increased growth and survival. Although predation was not documented as compensatory in these case histories, it may be in some systems where predators select other abundant prey when alewife are at low densities.

THREADFIN SHAD

The threadfin shad (*Dorosoma petenense*) was originally native to the east coast of Mexico and, without man's intervention, spread to U.S. Gulf Coast states by 1950. River impoundments apparently stabilized conditions enough for threadfin shad to invade parts of the Tennessee River from the Mississippi, and acclimatization or selection for cold-resistance permitted further expansion. Simultaneously, in the 1950s and 1960s, threadfin shad were stocked widely in reservoirs in Virginia, Georgia, Pennsylvania, California, Nevada, Arizona, Kansas, and New Mexico, although not successfully in all these places (Minckley and Krumholz 1960; Burns 1966; Beers and

McConnell 1966). Particular success and impressive invasions have occurred in Arizona and California, and the species has become established in the lower Ohio River. Threadfin shad are susceptible to cold kill, with a usual lower temperature limit of 7°C (Parsons and Kimsey 1954; McGee et al. 1977). Winter mortalities of threadfin shad are often demonstrated by increased power plant impingement (McGee et al. 1977; unpub. data, Duke Power Company, North Carolina).

The invasion abilities and recovery from winterkill of threadfin shad suggest it is often able to compensate quickly after a catastrophic event. About 200 yearling threadfin shad were introduced during May in Watauga Reservoir, Tennessee, and spawned soon afterward. By fall, large numbers of YOY came through powerhouse turbines, and many schools were observed in the reservoir (Parsons and Kimsey 1954). Even more impressive invasion abilities were demonstrated in the Colorado River. Two plantings totalling 1,020 fish were made in Lake Havasu. Within 18 months threadfin shad had populated all of the Colorado River from Davis Dam south to the Mexican border (about 370 km of river), including the Salton Sea and related irrigation canals (another 150 km - Cole et al. 1958 cited in Burns 1966). Large winterkills of threadfin shad are common in Lake Norman, North Carolina, since North Carolina is somewhat out of the shad's native range. However, some threadfin shad, mostly YOY, overwinter in heated discharges there, permitting repopulation each summer. During 1979-1982, population levels fluctuated between 200-600 million in summer and 2-30 million in spring in Lake Norman (Siler et al. in press). Up to 8 million threadfin shad per year have been impinged at Marshall Steam Station on Lake Norman, mostly during winter mortalities, and each year the population recovers (Siler et al. in press; unpub. data, Duke Power Co.). This demonstrates the potential explosive increase of this species. Similarly, in Montrose Lake, Missouri, winter survival of the threadfin shad population is thought to depend on a thermal plume (Pflieger 1975). Although mostly YOY threadfin shad were observed to survive winterkills in Lake Norman, larger individuals appeared to survive cold better in Watts Bar Reservoir, Tennessee (Adams et al. 1982). These shad used a relatively warm spring-fed cove as a thermal refuge. As in Lake Norman, the population recovered year after year from catastrophic winterkills, although changes in size frequency and gill net catch indicated a possible decline in abundance (McLean et al. 1981).

Age at Maturity

Threadfin shad live no more than 4 years in central Arizona reservoirs (Johnson 1971), and few reach 2 years in the Tennessee River (Parsons and Kimsey 1954). However, age at maturity fluctuates widely within that short lifespan. Age at first spawning is variously reported as, occasionally, young of the year (Berry et al. 1956 cited in Johnson 1971; Kimsey et al. 1957; McConnell and Gerdes 1964), 1 year (Parsons and Kimsey 1954; Johnson 1971), or as high as 3 years (Kilambi and Baglin 1969). Yearlings in Arizona reservoirs spawned later in the season than older fish (Johnson 1971). Late larvae may be subject to more predation or stress because of smaller size than early cohorts, but timing of food abundance relative to hatching is also important

in determining early survival and was not investigated. Johnson (1971) found YOY as large as some spawning fish (>49 mm), but the gonads of the YOY were not developed. Kimsey et al. (1957) and McConnell and Gerdes (1964) did not have proof of YOY spawning, but felt that late-occurring larvae and large-sized YOY were evidence for this. Gonad maturation indices showed multiple spawns during a year by individual fish, which would account for late-occurring larvae in that population (Johnson 1971). The only case of apparent compensatory change in age at maturity was given by Kilambi and Baglin (1969). In Beaver Reservoir, Arkansas-Missouri, where threadfin shad were introduced 3 years previously, they matured at 1-2 years, while in Bull Shoals Reservoir where fish were stocked 6 years before, they matured at 2-3 years. Population abundance was not given in this paper, but the Beaver Reservoir population may not yet have finished expanding to carrying capacity, so that its age at maturity reacted in a density-dependent manner. Bull Shoals Reservoir was also 11 years older than Beaver Reservoir, suggesting a potential difference in the biological community, and thus in food supply which could adversely affect shad.

Age of threadfin shad may be underestimated because of timing, or complete lack of annulus formation during a season. Threadfin shad in two Arizona reservoirs formed annuli usually from March to July, depending on age-group or size, but during one year, a year class with a history of poor growth had not added an annulus by October (Johnson 1970).

Fecundity

Threadfin shad fecundity in two Arkansas-Missouri reservoirs increased geometrically with length and linearly with weight (Kilambi and Baglin 1969); thus age-specific fecundity may be a compensatory mechanism if growth is density-dependent. A 100-mm female may contain from 6,700 to 12,400 eggs (Burns 1966). Kilambi and Baglin (1969) found a wide range of fecundities, from about 2,300 eggs for an 83-mm fish to 25,000 eggs for a 152-mm fish. Arizona threadfin shad 79-119 mm had 923 to 8,540 eggs (Johnson 1971). The latter two studies used a different minimum size for an egg to be considered mature, accounting for Johnson's somewhat lower estimates. However, Johnson did not have many large fish (>120 mm) to compare with those of Kilambi and Baglin. Johnson (1971) found gonadal aberrations of three types, all more common in larger fish: failure of one ovary to produce eggs, no recruitment ova or primary oocytes present after spawning (thus no preparation for future spawning), and gonads filled with fatty tissue. About 77% of the threadfin shad larger than 99 mm SL (131 mm TL) had fatty gonads. Thus, in some waters at least, the increase in fecundity with size is limited, perhaps a type of senescence.

Threadfin shad, particularly fish over 1 year old, may be capable of spawning twice a year, as demonstrated by egg diameter frequencies and presence of larvae in late summer (Kilambi and Baglin 1969; Johnson 1971). After Saguaro Lake, Arizona, was drained and refilled, the shad population re-established itself the next season, and larvae appeared in late summer. Two

spawns per year thus may be a density-dependent response. The second seasonal complement of eggs was apparently resorbed in other Arizona lakes, and in Saguaro Lake during other years (Johnson 1971).

Incubation Mortality

Threadfin shad eggs fertilized and incubated at densities $<1/\text{mm}^2$ in the laboratory showed a range of hatching success from 0 to 100% (McLean et al. 1981). However, eggs incubated at densities $>1/\text{mm}^2$ (eggs touching each other or in layers) all showed hatching success less than 15%. After about 40 h, viable eggs developed pigmented eyes, but only eggs in the top layer reached this stage of development. Fungal growth was frequent and denser at higher egg densities. In a large population, threadfin shad may deposit eggs in large masses which, as shown in McLean's experiments, may be subject to decreased hatching success. Thus, density-dependent egg mortality may be a compensatory mechanism for threadfin shad (McLean et al. 1981).

Growth

The threadfin shad does not attain a large size. Maximum size in Louisiana was about 200 mm (Lambou 1965), while fish in Arizona reservoirs attained 160-175 mm maximum (McConnell and Gerdes 1964; Beers and McConnell 1966; Johnson 1970). Threadfin shad in salt water may reach 236 to 257 mm (Kimsey et al. 1957; Finucane 1965, cited in Johnson 1970). Duke Power Company has unpublished growth data for Lake Norman threadfin shad. First-year growth varies widely (Table 7). Mean temperatures and time of spring warming appeared to control growth of all age-classes in the Arizona lakes studied (Johnson 1970), with one notable exception: a case of apparent density-dependent growth in Saguaro Lake. Growth of threadfin shad in the three reservoirs studied had been similar until Saguaro was drained and refilled in 1966. Growth of the 1967 year-class far exceeded the average because of an extended growing season, not because growth per month increased. Modal length of YOY was in the 50-60 mm TL range in all three lakes in July, but growth in Saguaro Lake continued through winter. YOY attained modal lengths of 73 mm by November and 88 mm by March 1968, while spring modal lengths stayed below 66 mm in the other two lakes. Johnson (1970) attributed the increased growth to lack of intraspecific competition. In these lakes YOY generally segregate from older threadfin shad for several months. Later in the year, YOY begin to inhabit the same areas as older fish and YOY growth stops about that time. During 1967 in Saguaro Lake, the few adult shad that had survived drainage were not a competitive threat to their offspring, thus YOY growth continued through the time when it would normally be halted, probably by competition for food. Growth of both the 1967 and 1968 year classes stopped at a "normal" time in 1968, thus stabilization was approached in 1 year. However, few 1968 YOY were collected, possibly indicating competitive suppression by the 1967 year-class. Johnson (1970) also pointed out that year-class strength and growth did not always act in a density-dependent manner in the three lakes. Temperature and possibly food availability affect growth and may confound attempts at correlation.

Threadfin shad were introduced into Bull Shoals Reservoir, Arkansas-Missouri, in 1961, and growth was studied from 1963 to 1966. First-year growth was greatest in 1963, when the population was still expanding. Females and males were 22 and 19 mm longer than the 4-year mean respectively. First-year growth was least in 1964, 11-12 mm below the mean, and corresponded with a large year-class (Bryant and Houser 1968). However, apparent slow growth may have been due to a late spawn and hatch resulting in more small fish.

TABLE 7. First-year growth (mm total length) of threadfin shad.

Length	Time represented, months	Location	Source
45 (mode) ~30-60 (range)	3	Pena Blanca Lake, Arizona	McConnell and Gerdes (1964)
~76 (mean) 45-85 (range)	3 to first annulus	Lake Havasu, California	Burns (1966)
73 (mode)	6-7	Saguaro Lake, Arizona, after lake drained and refilled	Johnson (1970)
88 (mode)	10-11		
51 (mean) 43-56 (range)	3-4	Roosevelt Lake, Arizona	Johnson (1970)
53 (mean) 37-56 (range)	3-4	Apache Lake, Arizona	Johnson (1970)
80-100	6-9	Watts Bar Reservoir, Tennessee	McGee et al. (1977)
65 (back-calculated)	entire growing season	Bull Shoals Reservoir, Arkansas-Missouri	Bryant and Houser (1968)

Competition

Threadfin shad in Lake Norman, North Carolina, apparently exhibited density-dependent mortality due to competition. In October 1979, the threadfin shad population was estimated at 304 million; mean shad biomass increased from 16.5 to 21.2 kg/hectare and estimated mortality was 38% from October to December. In contrast, in October 1980 the estimated population was 590 million; from October to December 1980 mean shad biomass decreased from 26.5 to 17.6 kg/hectare and estimated mortality was 67% (Siler et al. in press). Also, threadfin shad abundance was usually related to phytoplankton standing crop. Thus, Siler et al. (in press) believed that threadfin shad abundance was regulated by intraspecific competition during summer and fall. Winter mortality was due to cold and was density-independent as mentioned previously.

In addition to the above examples of intraspecific competition, the threadfin shad is believed to compete with kokanee salmon (*Oncorhynchus nerka*) in Shasta Lake (Burns 1966) and with young centrarchids in Pena Blanca Lake, Arizona (McConnell and Gerdes 1964), several Florida lakes (Philippp 1964), and in Millerton Lake, California (Burns 1966). In the latter case, growth rates of largemouth bass (*Micropterus salmoides*) younger than 3 years decreased after shad introduction. In the six Florida lakes selectively rotenoned to remove threadfin and gizzard shad (*Dorosoma cepedianum*), threadfin were successfully reduced in three lakes. Largemouth bass increased in both numbers and size in one lake, decreased in size but increased in numbers in another, and increased in size but decreased in number in the third (probably because some bass were rotenoned). In all three lakes where threadfin shad were reduced, gizzard shad increased even though gizzard shad were also a target of the rotenone program (Philippp 1964). Thus gizzard and threadfin shad may sometimes compete, although they coexist in many situations with no demonstrated niche shifts. Both are filter-feeders, with gizzard shad perhaps tending to feed more on phytoplankton than threadfin shad do. In two of the other lakes, threadfin shad catch remained about the same after rotenoning. In the sixth lake, where no gizzard shad were present, threadfin actually increased after poisoning, in both numbers and weight but especially numbers (from 1.4 to 12.8% of the catch - Philippp 1964). Apparently threadfin shad were able to compensate in some of these lakes, although the exact mechanism is unclear; perhaps decreased competition permitted increased survival.

Lake Beulah, Florida, was selectively rotenoned four times during 3 years. An estimated 411 kg of threadfin shad were killed during the first poisoning, and none were taken in the following three experiments (Huish 1957), demonstrating failure to compensate, as it appeared unlikely that every shad in the lake was killed. A total of 15,309 kg of gizzard shad were also killed, progressively less during the four poisonings. Increased growth rates and successful reproduction of gizzard shad may indicate it compensated at the expense of threadfin shad; data on other species were not available (Huish 1957).

Predation

Failure to compensate or compensatory predation was seen in two cases where introductions were made. Threadfin shad, largemouth bass and black crappie (*Pomoxis nigromaculatus*) were stocked in 1958 in Pena Blanca Lake, Arizona, then sampled the next 4 years. No YOY threadfin shad were collected in 1961, or yearlings in 1962, despite limnological and weather conditions similar to previous years when YOY were abundant. Eggs collected in 1961 hatched successfully in the laboratory. Reasons for the apparent failure were believed to be both predation and competition: 1961 was the first year that yearling black crappies were abundant, and adult threadfin shad were also more abundant than in previous springs (McConnell and Gerdes 1964). The largest adult threadfin shad of the study, up to 175 mm, were taken in April 1962 (maximum size in other years was about 160 mm); perhaps threadfin shad took advantage of the absence of a 1961 year-class.

The other case of compensatory predation was in Santee-Cooper Reservoir, where millions of threadfin shad existed prior to the establishment of striped bass. However, striped bass preyed on shad to the extent that shad could no longer support the bass population, and 30-50% of the striped bass died of starvation (Stevens 1964 cited in Burns 1966).

Density-independent predation was accomplished by stocking in Millerton Lake, California. Threadfin shad and striped bass (*Morone saxatilis*) were introduced in the 1950s to remedy poor centrarchid fishing. Although some natural recruitment of striped bass occurred, they could not control the shad and a huge shad population built up. Additional striped bass were stocked from 1972 to 1976, resulting in a 90% reduction of YOY threadfin shad in 1976 and 1977 and an increase in length of harvested bluegill (*Lepomis macrochirus*), although the 1976-1977 drought may have complicated analysis (McCammon and von Geldern 1979).

In two lakes where grass carp (*Ctenopharyngodon idella*) removed large amounts of vegetation, threadfin and gizzard shad biomass increased; however, in several other lakes, vegetation removal appeared to induce fluctuations in shad biomass (Bailey 1978). The mechanism responsible was not demonstrated, but may have involved vulnerability to predation after removal of cover, or changes in the dominant primary producers from macrophytes to phytoplankton (shad food supply).

Summary

There is some evidence for density-dependent growth, fecundity, age at maturity, and ability to spawn twice in 1 year for threadfin shad. Predation and both intra- and interspecific competition are believed to affect population levels, although predation was compensatory in two cases. No evidence was found for compensatory responses in sex ratio, egg deposition, disease, parasitism, cannibalism, starvation, or agonistic behavior. Cold mortality was not believed to be related to density, but in some cases appeared to be related to fish size.

Population explosions of threadfin shad in new habitats or after mass mortalities occur so rapidly (often 1 year) that growth, fecundity, and increased number of spawnings per fish may not be sufficient explanations, as these operate to increase stock between generations and not within one generation. Also, the physical limitations to growth, fecundity, and number of spawnings are reached sooner than the limit to survival; since survival of other shad species is usually less than 1% from hatching to the next year (Crecco et al. 1983; Mansfield and Jude in press), there exists a great deal of room for survival to increase. Increased survival of young as a result of decreased intraspecific competition (no established adult population) is an immediately operating mechanism that could account for explosive increases in abundance; however, survival has not been quantified for threadfin shad. The quick response of threadfin shad to catastrophe demonstrates it to be a resilient species.

GIZZARD SHAD

Introduction

The gizzard shad (*Dorosoma cepedianum*) ranges from southeastern South Dakota through the Great Lakes drainage to southern New York, southwestward to New Mexico and north-central Mexico and south along the Atlantic slope to the Gulf Coast (Miller 1960; Jester and Jensen 1972). It has extended its range by moving through canals, particularly to enter Lakes Michigan and Erie (Miller 1957, 1960). Gizzard shad increased greatly in abundance between 1950 and 1965 in Lake Erie (Bodola 1966). Along the northern part of its range, the gizzard shad is particularly susceptible to cold kills. It expands northward during warm years and then may undergo mass mortalities during a cold year, but is able to persist in areas such as the Great Lakes (Miller 1957). Gizzard shad, like threadfin, are attracted to warm effluents (particularly young shad - Gammon 1971), and after becoming acclimated to warm water may be more vulnerable to upwellings of cool water or may be dependent on a thermal plume (Great Lakes Fishery Laboratory 1970). Gizzard shad acclimated to 15-20°C water lost equilibrium within a few minutes of exposure to 6-7°C water, thus these fish would not have escaped cold water, even though they did not die for hours (Cox and Coutant 1976).

There are many examples in the literature of gizzard shad mass mortalities related to cold. Gizzard shad in a 29°C thermal plume from an Illinois corn products manufacturing plant were suddenly exposed to 0°C water because of plant slowdown, and a mass mortality resulted (Agersborg 1930). Some gizzard shad died at Port Sheldon, Michigan, when an upwelling lowered water temperature in the thermal plume from 22 to 14°C (Great Lakes Fishery Laboratory 1970). YOY gizzard shad usually die first at temperatures below 3.3°C in New Mexico, and older shad succumb later, primarily below 2.2°C (Jester and Jensen 1972). A sudden drop in air temperature, and river inflow of 0°C, led to a mortality of millions of fish, mostly shad, in Norris Lake, Tennessee (Wickliff 1953). Shad may be particularly impacted by water <4°C because it is less dense than >4°C water, thus it floats at the surface where shad may congregate. Gizzard shad die-offs are sometimes attributed to warm

temperatures or a difference between carbon dioxide tension of surface waters and the CO₂ partial pressure of the air (Wickliff 1953; Miller 1960).

However, the die-offs in question, at Erie, Pennsylvania and Norris Lake, also occurred during winter, suggesting that cold stress may have had some effect.

There are several other possible causes of mass gizzard shad mortalities. During drawdowns of Elephant Butte Lake, New Mexico, extensive gizzard shad mortalities were attributed to nitrogen bubbles caused by bacteria, *Aerobacter aerogenes*. *Aerobacter* is normally harmless to fish, but causes a gas-bubble disease when fish are subject to stress such as crowding (Jester and Jensen 1972). Parasitism or fungus may cause mortalities, or may be a secondary infection after shad are weakened (Miller 1960). Gizzard shad were apparently avoiding the strong current of the Detroit River when they ran up an intake pipe of the Parke-Davis Company, Detroit, Michigan, and 2-3 tons were killed by the plant (unpub. report, Inst. Fisheries Research, MDNR, Ann Arbor, MI). Mass spawning mortalities were reported in two Florida lakes by Moody (1957). Gizzard shad finished spawning in May in Lake Panasoffkee, and the largest fish disappeared from the catch. In May 12% were over 356 mm TL, while in June and July only 1% were >356 mm (Moody 1957). Although Moody reports a large concurrent reduction in numbers, catch data do not appear to be adjusted for number of samples taken, which were fewer in June than May.

Spills of fly ash slurry and sulfuric acid occurred a few years apart in the Clinch River near Carbo, Virginia, decimating fish populations. The slurry reduced index catches by 79% in numbers and 72% in weight, while the acid killed about 5,300 fish. Effects were noted for 120 km and 21 km downstream respectively. Gizzard shad comprised 19.6% of the catch before the first kill, and 54.5% immediately post-kill. The increased percentage suggests better ability to withstand or recover from toxic spills (and, perhaps, compensate) than the other species present, primarily suckers, sunfishes, and minnows (Raleigh et al. 1978). Gizzard shad have the ability to rapidly invade new environments, demonstrated by their increase in abundance and dominance in Clearwater Lake, a new reservoir in Missouri (Patriarche and Campbell 1957), their increase in the Great Lakes, and in many other lakes where they have "overpopulated" (Miller 1960). Their potential for increase, sometimes at the expense of other species, appears to be strong.

Growth

Growth of gizzard shad is highly variable among sites (Tables 8, 9). The fastest growth rate was reported by Bodola (1966), for Lake Erie gizzard shad, 258.7 mm to the time of first annulus formation and 107.1 mm to the second. Subsequent yearly increments are comparable to or smaller than those at other sites. However, the first 2 years' growth keeps Lake Erie shad larger than shad at other sites except for Upper Spavinaw Lake, Florida, where the third-year increment is 130 mm (Tables 8, 9). The slowest first-year growth, 75.8 mm, is reported for Conchas Lake, but larger subsequent increments bring those fish to a size similar to fish at other sites (Table 9). In many cases, growth rate and length of life have an inverse relationship (Table 9).

TABLE 8. Mean total lengths and length ranges (mm) for each age-group of gizzard shad from several locations.

Location, time and source	Age-group					
	0	1	2	3	4	5
Lake Beulah, Florida (Huish 1957) ¹						
March 1955			227			
			178-267			
March 1956		118	251			
		89-165	229-304			
July 1956	101					
	76-127					
July 1957	133	238				
	114-178	216-254				
Elephant Butte Lake, New Mexico (Jester and Jensen 1972) ^{2,3}						
1962-1963	108	173				
1964	108	155	221			
1965	96	172	188	250		
1966	90	162	213	218	279	
1965-1966 ⁴	86	128	156	185	214	
1970	94	150	183	219	254	
Clearwater Lake, Missouri (Patriarche and Campbell 1957) ³						
1947		(124)	(36)	(30)	(15) ⁵	
1948	163	216	249	272	297	312
		(53)	(33)	(23)	(25)	(15)
1949	152	216	249	272	289	
		(64)	(33)	(25)	(15)	
1950	163	249	279	304		
		(86)	(30)	(25)		
1951	152	292	315			
		(140)	(23)			
Chickamauga Reservoir, Tennessee (Eschmeyer et al. 1944)						
Fall 1942	90	190				
April 1942			216			

TABLE 8. Continued.

Location, time and source	Age-group					
	0	1	2	3	4	5
Upper Spavinaw Lake, Oklahoma (Jackson 1957) ³						
1952-1954	196	307	437			
Lower Spavinaw Lake, Oklahoma (Jackson 1957) ³						
1952-1954	165	224	264	297	325	
Missouri River, Nebraska (Hesse et al. 1976) ¹						
1971-1975	139	285				

¹ Calculated from length-frequency tables; fish not aged.

² Large mortality due to drawdown in 1964.

³ Lengths represent entire growth season; back-calculated lengths at time of annulus formation the following year.

⁴ Unpublished data, R.R. Patterson, New Mexico State University.

⁵ Length increments in parentheses.

We found several examples of density-dependent growth for gizzard shad. Although mass mortalities in Elephant Butte Reservoir were not reflected in sudden growth increases, predation pressure did result in increased growth. As catch per unit effort of gizzard shad declined 62% over 7 years, mean weight of the fish increased in 3 years from 57 to 85 g, then leveled off at 74-76 g in following years (Jester and Jensen 1972). Lengths during 1965-1966 were less than lengths in 1970 (Table 8), although the 1965-1966 data were from a different study (perhaps different methods), and back-calculated growths do not show the same trend.

In 1948, the first year of impoundment of Clearwater Lake, Missouri, gizzard shad produced a large year-class that dominated catches from 1948 to 1952. First-year growth (age 0) was 163 mm in 1948 and was not surpassed in subsequent years (Patriarche and Campbell 1957; Table 8). However, 1949 growth of the 1948 year-class (53-mm increment) was well below average, probably a density-dependent response. Growth increments in following years were close to the average.

TABLE 9. Grand mean lengths (upper line) and increments (lower line) in mm at time of annulus formation for gizzard shad at various locations. From Jester and Jensen (1972).

Locality (Author and date)	Grand Mean Lengths and Increments at Formation of Annulus --										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Elephant Butte Lake, N.M.	94.4	150.6	183.3	218.6	253.9	273.0	291.0	323.8			
(Jester and Jensen, new data)	94.4	56.1	32.8	35.3	35.3	19.0	18.0	32.8			
Elephant Butte Lake, N.M.	85.9	127.9	156.0	184.8	213.7	233.5	238.4	259.5			
(Patterson, 1968)	85.9	42.0	30.2	24.6	23.0	17.7	14.0	9.5			
Conchas Lake, N.M.	75.8	153.8	225.0	284.3	320.0	342.5	360.3	370.8			
(Jester, 1962)	75.8	78.0	71.2	59.3	35.7	22.5	17.8	10.5			
Grand Lake, Okla.	100.0	202.5	260.0	317.5	350.0	382.5	395.0				
(Jenkins, 1963)	100.0	102.5	57.5	57.5	32.5	32.5	12.5				
Tenkiller Reservoir, Okla.	140.0	237.5	350.0	385.0	422.5	422.5					
(Hall and Jenkins, 1953)	140.0	97.5	112.5	35.0	37.5	0					
Fort Gibson Reservoir, Okla.	142.5	257.5	325.0								
(Jenkins, 1953)	142.5	115.0	67.5								
Spike Lake, Okla.	160.0	225.0	305.0								
(Hall, 1951)	160.0	65.0	80.0								
Poteau River, Okla.	197.5	227.5	310.0	330.0	357.5						
(Hall, 1951)	197.5	30.0	82.5	20.0	27.5						
Lake Erie	258.7	365.8	402.6	429.3	467.4	428.4					
(Bodola, 1965)	258.7	107.1	36.8	26.7	38.1	-39.0					
Foots Pond, Ind.	190.0	247.5	265.0	282.5	347.5						
(Lagler and Applegate, 1942)	190.0	57.5	17.5	17.5	65.0						
Grassy Pond, Ind.	192.5	227.5	257.5	282.5	295.0						
(Lagler and Applegate, 1942)	192.5	35.0	30.0	25.0	12.5						
Crab Orchard Lake, Ill.	100.8	136.1	167.1	170.1	162.5						
(Lewis, 1953)	100.8	35.3	31.0	3.0	-7.6						
Beaver Dam Lake, Ill.	240.0	277.5	330.0	375.0							
(Lagler and Van Meter, 1951)	240.0	37.5	52.5	45.0							
Lake Wappapello, Mo.	102.5	170.0	207.5	230.0	245.0	257.5	272.5	292.5	300.0	292.5	
(Patriarche, 1953)	102.5	67.5	37.5	22.5	15.0	12.5	15.0	20.0	7.5	-7.5	
Herrington Lake, Ky.	109.5	196.0	259.0	311.0	334.3						
(Turner, 1953)	109.5	86.5	63.0	53.0	23.3						
Lake Newnan, Fla.	253.6	316.7	338.2								
(Berry, 1955)	253.6	62.0	22.6								

Gizzard shad growth was more rapid in a new reservoir, Upper Spavinaw Lake, than in a 29-year-old reservoir, Lower Spavinaw Lake, Oklahoma (Jackson 1957; Table 8). The mean (1952-1954) growth increments for the second and third year were particularly large compared to other sites. Jackson (1957) states that growth of the 1952 year class (the year of impoundment) was very poor in 1954, indicated by time of annulus formation, and he believed intra-year-class competition was responsible. However, he presented only mean sizes over 3 years, so density-dependent growth could not be quantified.

Lake Beulah, Florida, was selectively rotenoned to remove shad four times over 3 years. The four poisonings removed 10,555, 3,589, 688, and 477 kg of gizzard shad respectively, and 411 kg of threadfin shad in the first poisoning only (Huish 1957). Samples of gizzard shad from the poisonings indicated increased reproduction and growth (Table 8). No yearlings were collected during the first poisoning. Sizes of yearlings increased greatly from the second to fourth poisonings, and sizes of YOY increased from the third to fourth (Table 8).

Condition

Gizzard shad coefficient of condition in the Missouri River varied from 0.849 in April to 1.081 in October, generally increasing from spring to fall (Hesse et al. 1976). Gizzard shad in Elephant Butte Lake had a mean coefficient of condition of 0.867 for 1965-1970. Condition was highest in 1965 (0.965) and lowest in 1967 (0.814) and was not directly related to population changes as shown by catch per effort (Jester and Jensen 1972). The 1964 mortality due to drawdown may have had a density-dependent effect on the condition of fish collected in 1965, but 1964-1965 catch per unit effort was higher than any subsequent year to 1970. Jester and Jensen (1972) noted that mean condition in Elephant Butte Lake was lower than any other water, including Foots Pond, Indiana (Lagler and Applegate 1942), Herrington Lake, Kentucky (Turner 1953), the Spavinaw Lakes (Jackson 1957), and Lake Erie (Bodola 1966). No density-dependent relationships were apparent at those sites, except possibly at the Spavinaw Lakes where gizzard shad in the new reservoir achieved a given weight (225 g) at a shorter length (284 mm) than those in the 29-year-old reservoir (292 mm - Jackson 1957).

Fecundity and Age at Maturity

Unlike alewife or threadfin shad, the gizzard shad shows declining fecundity with age, and with size beyond 500-600 g. Bodola (1966) found precocious age-1 fish from Lake Erie to have the fewest eggs, 22,400-96,560, while age-2 fish had the most, 211,380-543,910 eggs (mean = 378,990) at fish sizes of 282-305 mm and 524-593 g. Fish of ages 3 to 6 showed declining fecundity, although Bodola (1966) took data from only 13 fish. Average fecundity of three 3-year-olds was 344,780 eggs; of two 4-year-olds, 308,750; and one 6-year-old had 215,330 eggs. The 3- to 6-year-old fish all were >322 mm and >700 g (Bodola 1966). A few 3-year-old shad were immature. Gizzard shad in Elephant Butte Lake showed a similar declining trend in fecundity with

age. Shad matured at 2 or 3 years. Twenty-six age-3 fish had fecundities from 28,545 to 70,874 (mean 40,500), while three age-4 fish had 27,815 to 31,396 eggs (mean 29,884). The one 6-year-old shad had 58,467 eggs, but its ovarian weight was only about 6% of total body weight, in contrast to 9-13% for 3-year-olds. Regressions using size and age of fish were all negative, indicating declining fecundity. The highest correlation coefficient was obtained for a regression including length, weight, and fecundity (Jester and Jensen 1972). Declining fecundity with age and size indicates fecundity is probably not a compensatory mechanism for gizzard shad, at least not in the same way as other species where attaining a larger size permits more eggs to be produced. Reproductive senescence may occur for gizzard shad as for threadfin; gonads of old fish may contain more connective or fatty tissue. The only comparison that can be drawn is the greater fecundity of Lake Erie shad than those from Elephant Butte Lake. The other notable difference is the faster growth and larger ultimate size of Lake Erie gizzard shad. Habitat, including food supply, influences growth and egg production. We have no evidence that the fecundity difference between the two populations is density-dependent. Age at maturity has not been shown to be density-dependent.

Egg Deposition

Gizzard shad in good condition in Melvern Reservoir, Kansas, spawned earlier in the season than those in poorer condition. Early spawners may have spawned more than once during the season (Willis 1984). This could be a density-dependent response, but complete data have not been published.

Competition

Like threadfin shad, gizzard shad are believed to compete with centrarchids. In pond experiments with largemouth bass and bluegill, the average weight of adult bluegill was 79 and 62 g in two ponds with gizzard shad and 121 g in a pond without shad (Swingle 1949). Additionally, during the second year in the pond with all three species, there was little gizzard shad reproduction, probably due to high densities of large shad, bluegills, or both (Swingle 1949).

A comparison of two similar lakes in Oklahoma showed that five out of the six most abundant species (all centrarchids) in a lake without gizzard shad present, displayed faster growth, better condition, and a greater average length than the same species in a similar lake with gizzard shad (Jenkins 1957). The exception was largemouth bass. This effect was most notable for black crappie and redear sunfish (*Lepomis microlophus*). Black crappie reached 81 mm in 1 year and 231 mm in 4 years in the lake with gizzard shad, and 114 mm in 1 year and 272 mm in 4 years in the lake without shad. For redear sunfish, 1-year and 6-year lengths were 109 and 221 mm respectively in the shad lake, and 142 and 257 mm in the lake with no shad. Coefficients of condition were 12-19% lower in the shad lake for redear sunfish, and 10-28% lower for black crappie. Average lengths were 8 mm greater for black crappie

and 18 mm greater for redear sunfish in the lake with no shad (Jenkins 1957). These differences could not be attributed to physical, chemical, or biological characteristics of the lakes other than presence of gizzard shad.

Other species believed to compete with gizzard shad are common carp (*Cyprinus carpio*) and threadfin shad. When gizzard shad were selectively removed from Black Hawk Lake, Iowa, as the percent by weight of shad declined from 98.1 to 2.8%, the percent by weight of carp increased from 1.8 to 96.3% (Rose 1957 cited in Miller 1960). This suggests that gizzard shad had been successfully out-competing common carp until the removal operation. Threadfin and gizzard shad may also compete, as shown by the data of Huish (1957) and Phillippy (1964) - see THREADFIN SHAD, Competition.

There are several case histories that show evidence of intraspecific competition for gizzard shad, primarily where removal or new introductions of shad resulted in faster growth or better recruitment than usual. After removal of 10,000 adult gizzard shad from Black Hawk Lake, Iowa in 1950-1951 and stocking of predators in 1951, about 18,400 young shad per hectare were removed in fall 1951 (Rose 1957 cited in Miller 1960). Increased survival of young due to decreased competition was probably responsible for this successful recruitment. Similarly, increased abundance and size of YOY gizzard shad in Lake Beulah was probably due to removal of many shad (Huish 1957). In two of the six Florida lakes that were selectively rotenoned to remove shad, numbers of shad increased while biomass stayed the same or did not increase in proportion to numbers (Phillippy 1964). A total of 70,777 kg of gizzard shad was removed from Lake Panasoffkee, Florida in 1 year. There was no apparent trend in catch per unit effort of gizzard shad during that time, although catch was expected to decline (Moody 1957). Relatively constant catches indicate gizzard shad apparently compensated for the losses, but the mechanism is unknown.

In Swingle's (1949) pond experiments, gizzard shad reproduced abundantly in the first year, but apparently did not in the second year when fish densities were high. The aforementioned growth rate and condition differences of gizzard shad in Lower and Upper Spavinaw Lakes probably reflect intraspecific competition differences between an old reservoir with an established population and a new reservoir with an expanding population (Jackson 1957). Clearwater Lake, Missouri, also demonstrated this phenomenon; during the first year of impoundment a large year class of gizzard shad was produced, which dominated gill net catches for 4 years thereafter, but showed slow growth in its second year. Seven years after impoundment, the fish populations were stabilized and gizzard shad age distributions had become more balanced (Patriarche and Campbell 1957).

Predation

Striped bass were introduced into Keystone Reservoir, Oklahoma in 1965 and began natural reproduction by 1970. Standing crop of gizzard shad fluctuated between 290.6 and 2,067.2 kg/hectare during 1971-1979, but there was no downward trend, despite gizzard shad representing 83% by volume of

striped bass food (Combs 1980). Thus gizzard shad must have compensated for predation mortality. Gizzard shad >178 mm declined from 27% to 1% of the total catch during 1971 to 1979. Shad eaten by striped bass were 25-241 mm with a mode of 76 mm. Thus the reduction in large shad was probably not entirely a result of predation; some environmental factor may have contributed (Combs 1980).

The 1953 year-class in Lower Spavinaw Lake was greatly reduced and was outnumbered by yearling 1952 fish in a fall 1953 sample. Extreme low water in 1953 concentrated the population and may have permitted predators to take an increased proportion of the gizzard shad YOY (Jackson 1957). Removal of vegetation appeared to induce fluctuation of shad populations in some lakes (Bailey 1978), possibly because shad became more vulnerable to predation or the food base changed.

Summary

The gizzard shad is a resilient species, undergoing wide natural fluctuations in abundance and invading new habitats rapidly. There is some evidence for density-dependent growth and egg deposition, and for population regulation by competition and predation. Fecundity and age-at-maturity are apparently not density-dependent, and data are not available for other mechanisms. Like alewife and threadfin shad, the strongest compensatory responses occurred after catastrophes when populations showed increased abundance of young, probably partly due to decreased competition permitting increased survival. An added dimension for gizzard shad is their faster growth and much larger ultimate size, which take them out of the size range for prey sooner than alewife or threadfin; thus gizzard shad predation mortality may be related to density-dependent growth. Such a compensatory response may be what permits gizzard shad to out-compete threadfin shad when both are selectively removed from a lake.

LAKE WHITEFISH

Introduction

The lake whitefish (*Coregonus clupeaformis*) is distributed throughout Canada, the Laurentian Great Lakes, and fresh waters of the northern United States (Scott and Crossman 1973). Lake Erie represents the southern extremity of the whitefish range (Hartman 1972; Leach and Nepszy 1976). This species is a valuable food fish and is commercially exploited throughout its range. Lake whitefish are cold stenotherms which require silt-free spawning grounds for successful reproduction and cold, well-oxygenated, hypolimnetic waters for summer habitat (Leach and Nepszy 1976). Under natural conditions, lake whitefish are long-lived (up to 28 years - Scott and Crossman 1973), produce multiple spawns, and are thereby buffered against times of unfavorable environmental conditions (Christie 1972).

Factors (all of which are in some way attributable to man) which have been detrimental to whitefish populations (especially in the Great Lakes) during the last 150 years include overfishing, environmental deterioration, predation by the sea lamprey, and introduction of other species (Spangler 1970; Berst and Spangler 1972; Christie 1972; Hartman 1972; Lawrie and Rahrer 1972; Wells and McLain 1972; Regier and Hartman 1973). Some studies have shown resilience of whitefish populations and demonstrated their compensatory potential; however, in some systems the population has collapsed despite fishing pressure which was less intense than in other lakes with successful fisheries (Bell et al. 1977). Whitefish year-class variation can be great in amplitude and apparently random in frequency making it difficult to determine whether a decline in stocks is caused by overharvesting, cyclic phenomena, or environmental deterioration (Christie 1968). Some aspects of lake whitefish biology make lake whitefish subject to severe fluctuations under natural conditions, and increase their susceptibility to man-related stress factors. Specifically, lake whitefish spawning success is highly variable (especially in the southern part of their range), and depends on a fairly narrow range of temperatures during egg development and hatching. Year-class success was not related to size of spawning population, number of planted hatchery-raised fry, or such factors as turbidity, wind, precipitation, or water level (Lawler 1965). A climatic warming trend in the Great Lakes region over the past 50 years (Beeton 1961) may push lake whitefish north of Lake Erie, the present southern limit to their distribution. Lake whitefish and other coregonines form discrete populations and during spawning, less than 5 % of the fish will stray to other, even closely adjacent, spawning grounds (Cucin and Regier 1965; Christie 1972; Colby et al. 1972). This means that a depleted stock may be replaced only very slowly by adjacent stocks and perhaps not at all if the original stock is reduced substantially below a critical level (Colby et al. 1972). The reproduction of whitefish in the littoral zone makes them vulnerable to thermal pollution, nutrient loading, siltation, increased levels of chlorinated hydrocarbons, and heavy metals, as physically or chemically toxic effluents can be concentrated by prevailing onshore winds or other physical means (Berst and Spangler 1972).

Documentation exists showing that compensatory mechanisms are exhibited in lake whitefish populations although in many cases, such a myriad of influences is working on a population that it is difficult to distinguish which stimuli are bringing about which responses. Few studies document lake whitefish response to catastrophic events. Lake whitefish fisheries have collapsed and slowly recovered in the Great Lakes (Christie 1968; Kenyon 1978) and Lesser Slave Lake (Bell et al. 1977), but few data on compensation have resulted. The following presents the responses of lake whitefish to mortality, organized by compensatory mechanisms as we have defined them. We also include some information on other *Coregonus* species.

Compensatory Mechanisms

Growth--

Evidence for compensatory growth by lake whitefish when population densities were lowered was found by several investigators. In two similar Alberta lakes, Bidgood (1973) documented a higher growth rate of lake whitefish in the lake which had the lower whitefish density. Cucin and Regier (1965) inferred that periods of greater growth rates of lake whitefish in southern Georgian Bay were due to periods of decreased population density. Both in a survey of Northwest Territories lakes and in an experimental situation, Healey (1975, 1980) found that exploited populations of lake whitefish exhibited greater growth than unexploited populations. Lake whitefish growth rate increased 12 mm per year on the average when 30% of the population was removed for 2 consecutive years, which amounted to about 50% of the total population (Healey 1980). We consider this size population decrease to be a catastrophic event.

Other investigators reported less definitive or even conflicting results on the subject of compensatory growth, but inconsistencies are probably attributable to other interacting factors and stresses. Miller (1947) examined two lakes in Alberta and found that growth rate of the lake whitefish population of one lake increased when rate of exploitation increased, but the converse was not true: in the other lake, a period of reduced exploitation did not decrease growth rate. In Lake Ontario, Christie (1972) found no evidence of compensatory shifts in growth, recruitment, or survival when fishing pressure had brought abundance levels of whitefish well below carrying capacity. Lake whitefish in Lake Erie grew rapidly during the late 1920s when they were abundant but heavily fished (Kenyon 1978). The Lake Erie stock collapsed, but data from the 1970s show slower growth despite low population levels; slow growth was attributed to habitat degradation. However, weights of whitefish at given lengths were significantly greater in the 1970s than the late 1920s (Kenyon 1978), perhaps showing compensation in condition factor.

Survival--

Few studies addressed the question of changes in survival of lake whitefish in response to changes in population density, but two that did indicated that this factor does not operate as a compensatory mechanism for whitefish. In Lake Winnipeg, the lake whitefish population was subjected to overfishing, yet compensatory survival was exhibited such that as the population fell, survival rate decreased from 34 to 12% (Davidoff et al. 1973). In Lake Ontario, a decrease in abundance to well below carrying capacity did not affect survival rates (Christie 1972). In the population experimentally reduced by 50%, Healey (1980) found increased abundance of age-0 and age-1 lake whitefish. Abundance of these year classes was still evident 4 years after the experiment, showing improved recruitment which no doubt was related to survival during juvenile stages.

Fecundity--

Bell et al. (1977) found that fecundity was size-specific and not age-specific for lake whitefish in Lesser Slave Lake, Canada, so if growth works as a compensatory mechanism for this population, then fecundity would act as an interacting mechanism. Healey (1980) contended that whitefish fecundity may increase when populations are exploited.

Sex Ratio--

Exploitation of whitefish in Lesser Slave Lake brought about fluctuations in sex ratio as males matured earlier and suffered greater mortality (i.e., were exposed to the fishery earlier) than females (Bell et al. 1977). This does not demonstrate compensation. In two Alberta lakes from which whitefish were exploited at different rates, the sex ratio was proportionate, 1:1 (Bidgood 1973), but it was not clear what factors influenced this situation. Bloaters collected in Lake Michigan, however, were 99% female after heavy exploitation (Brown 1970). Although gear bias accounted for some of this female predominance, the sex ratio was undoubtedly unbalanced.

Age at Maturity--

In Lesser Slave Lake, Bell et al. (1977) documented that mature lake whitefish of a given age were considerably larger than immature fish of the same age, implying that maturity was size- not age-specific. Thus in conjunction with compensatory growth, age at maturity could act as a compensatory mechanism. Healey (1975) thought that heavily exploited whitefish stocks matured at both a younger age and possibly a smaller size, which would be evidence for age at maturity acting independently of growth as a mechanism of compensation. The evidence is not definitive however, and some studies indicated that age at maturity could not be considered compensatory. For whitefish in two Alberta lakes and in Lake Winnipeg, maturity seemed to be age-rather than size-dependent (Rybicki and Doan 1966; Bidgood 1973).

Cannibalism--

Bidgood (1973) documented that lake whitefish eggs comprised a major portion of whitefish diet from October through January in a lake that was overpopulated by whitefish; however, during December and January eggs comprised only a small portion of the diet of a less dense whitefish population in a nearby lake.

Disease--

No references were found relating disease to whitefish population density.

Predation--

Predation by sea lamprey has had a major effect on the decline of lake whitefish populations in Lake Superior (Lawrie and Rahrer 1972), Lake Michigan (Wells and McLain 1972), Lake Huron (Spangler 1970; Berst and Spangler 1972), and Lake Ontario (Christie 1972). Lamprey predation was not a major factor in the decline of whitefish populations in Lake Erie, perhaps because of a relative lack of streams suitable for lamprey spawning in the Lake Erie area (Hartman 1972). Control of sea lamprey in Lake Huron brought about increased survival, an increase in modal age, and a slight broadening of population age structure of lake whitefish (Spangler and Collins 1980).

According to Christie (1972), the stress exerted on prey stocks by lamprey increases as prey become numerically reduced, thus lamprey predation is compensatory. This apparently occurs, at least in part, because lamprey may turn to ever smaller prey as older, larger individuals become eliminated (by predation, fishing, or natural mortality) from the prey population, and the collapsing age structure of fish becomes incapable of adequate reproduction to maintain the stock. As an indirect effect on whitefish populations, destruction by sea lamprey of major predators of the Great Lakes (lake trout and burbot, *Lota lota*) allowed the flourishing of other species (alewife and rainbow smelt, *Osmerus mordax*) which had been controlled by the predators but which subsequently multiplied unchecked and competed with whitefish for food or preyed on whitefish young (Berst and Spangler 1972).

Parasitism--

Stress can make individuals more vulnerable to parasitism which in turn can cause further stress and affect density-dependent responses of fish. For example, Colby et al. (1972) found that in oligotrophic Canadian lakes, eutrophication sometimes resulted in an increased incidence of infestation of the parasite *Taenia* which is suspected to cause slow growth and high mortality of YOY coregonines.

Intra- and Interspecific Competition--

Compensatory mortality can result if young whitefish are suppressed by the adult stock. This may occur if older fish force young into marginal areas or habitats (Johnson 1976) or inhibit their normal exploratory and foraging activities (Healey 1980).

Of two lake whitefish populations in different lakes, the population which was subjected to a relatively greater intensity of intra- and interspecific competition for food existed on a relatively inferior diet in terms of both quantity and quality (Bidgood 1973). Dietary differences were reflected by differences in growth rates of individuals of the two populations, although age of maturity and fecundity were about the same for whitefish in either lake.

Whitefish populations sometimes produce an exceptionally strong year-class (Lawler 1965). Healey (1980) propounded that the presence of such a year-class may cause a decrease in the growth rate of the whole population presumably because competition for food becomes greater.

Looking at all cisco species in Lake Ontario, Christie (1972) noted a sequence of progressive loss from largest to smallest forms. The total biomass of ciscoes harvested by the fishery stayed close to the same through this period of loss however, because as bigger forms disappeared, smaller forms exhibited compensatory increases in reproduction, growth, and productivity.

Species in competition can be affected by indirect causes. Colby et al. (1972) gave the example of a lake where eutrophication caused oxygen depletion at the mud-water interface which changed the bottom fauna from animals such as *Mysis*, *Pontoporeia*, and mayfly larvae to chironomids and oligochaetes. Lake whitefish could out-compete other fish species for the food items available under the former conditions, but percids, centrarchids, and cyprinids all out-compete whitefish under the changed conditions.

Another example is given by Miller (1947) who described how a competitor species of lake whitefish could thrive if the older age-groups of whitefish were subjected to increasing fishing pressure while no such pressure was put on the competitor species.

Condition factor and egg deposition--

No references were found relating these subjects to compensation.

Summary

Lake whitefish exhibit the compensatory mechanisms of growth, size-specific fecundity, age at maturity, cannibalism of eggs, survival, and inter- and intraspecific competition. Under natural conditions these mechanisms help maintain whitefish populations. Complications arise because of the complex web of direct and indirect stresses caused mostly by man and his activities. Such stresses cause imbalances and make whitefish populations more vulnerable to other stresses, in the end having a snowball effect from which recovery by compensatory mechanisms may not be possible.

PACIFIC SALMON

Introduction

Population dynamics of the five *Oncorhynchus* species native to North American waters have been well studied because of the salmon's economic importance. Larkin (1977) gives a good review of their life histories and

mechanisms of population regulation. The sockeye salmon (*O. nerka*) in particular has much published information available; thorough treatments of various aspects are in Johnson (1965) and Foerster (1968). Although the native range of the *Oncorhynchus* species is the northern Pacific, several species have been stocked in fresh water and successfully spawned as landlocked populations. Large numbers of coho (*O. kisutch*) and chinook salmon (*O. tshawytscha*) have been stocked in the Great Lakes, and some natural recruitment has occurred although stocking continues. Pink salmon (*O. gorbuscha*) were released accidentally in Lake Superior and have spread to all the Great Lakes, with spawning populations common in northern Lakes Michigan and Huron in addition to Superior. Some life history patterns, and thus compensation potential, are different for landlocked salmon populations.

Catastrophic mortalities of salmon are often related to spawning migrations upriver. Obstacles to migration prevent fish from reaching their spawning grounds, thus eliminating that year class from the stream. Obstacles may be landslides, rockfalls, or dams. Low water can be a hindrance to migration. Delays in migration may cause the fish not to spawn, even if they finally do reach the spawning grounds (Larkin 1977). Nitrogen supersaturation below Columbia River dams resulted in pre-spawning mortality of summer-run chinook and sockeye salmon. Mortalities of chinook were estimated as high as 59% below the Wells Dam in 1967 (Meekin and Allen 1974). Similarly, migration of juvenile salmon downstream to the sea, or smolting, is affected by obstacles. Dams on the Snake River delayed migrations of juvenile chinook salmon and caused direct mortality by turbine passage and gas supersaturation, and indirectly caused mortality by slow migration through reservoirs and exposure to predation during low-flow years (Raymond 1979).

Spawning migrations in rivers and streams by salmon have led man to pay particular attention to early life stages, in contrast to other species for which the literature is not so well established. The requirements and mortality of salmon eggs have been found to have some density-dependent relationships.

Spawning Site Competition and Egg Deposition

Salmon excavate redds when spawning so that percolation through the gravel, and thus oxygen supply to the eggs, is enhanced. The first arrivals after migration choose the most favorable sites. At greater densities, some fish are forced to less favorable redds and there is more chance of late arrivals digging up the redds of those who came earlier (Foerster 1968; Larkin 1977). Such results clearly do not harm the adults but have a direct effect on survival of eggs. Percent survival of sockeye salmon eggs in Lake Dalnee, Kamchatka ranged from 1% when 52,800-73,100 females were present, to 72-79% when 9,300-38,000 females were present (Krogus and Krokhn 1948; Krogus 1951, both cited in Foerster 1968). Krogus (1951) attributed the 1% survival to digging up of early redds by later spawners. Semko (1954, cited in Johnson 1965 and in Foerster 1968) found sockeye salmon spawning at a high density retained 6% of their eggs and lost 37%, thus 57% were successfully deposited

in the redds. Egg retention may be as low as 0.5% for sockeye (Foerster 1968). Egg retention was not density-dependent in Hooknose Creek, British Columbia (Hunter 1959).

Incubation Mortality

Chum salmon (*O. keta*) eggs have an oxygen demand of 0.00013-0.0003 mg/egg/h at temperatures of 0.1-8.2°C. Measurements of oxygen within gravel interstices in Nile Creek, Vancouver Island, showed that oxygen was insufficient for eggs in some parts of the stream where dead eggs had been found (Wickett 1954). Droughts, floods, and particularly silting can increase egg mortality (LeCren 1965). Floods could dislodge eggs, permitting predation, while droughts or silting prevent oxygenated waters from reaching the eggs. These are basically density-independent forms of mortality. However, at high densities eggs are more subject to oxygen depletion or fungus infection (Johnson 1965; LeCren 1965), or buildup of carbon dioxide (Foerster 1968) or nitrogenous wastes (Hunter 1959). Egg losses during incubation are greater at high densities, whether due to dislodging, predation or oxygen depletion (Foerster 1968). Accumulation of adult carcasses may increase oxygen depletion as well, due to decomposition (Foerster 1968). Losses during incubation may range from 70% to 100% (Larkin 1977). Population density in Hooknose Creek affected pink and chum salmon survival from egg to fry, while temperature, stream discharge, and sex ratio did not affect survival perceptibly. Egg and alevin mortality was 70-80% at low density (<500 eggs/m²) and >90% at densities >1,500 eggs/m² (Hunter 1959). Compensatory mortality during spawning and incubation is considered to be one of the important population regulators for pink and chum salmon (Neave 1953).

Predation

Predation on salmon fry is one of the most significant mortality factors, but is generally not compensatory. Because the predators inhabit the streams year-round, they are not dependent on salmon fry for food and their numbers are not limited by salmon fry. Thus the predators take a fixed quantity of fry as prey, regardless of fry densities, a depensatory effect (Neave 1953; Hunter 1959; Johnson 1965; Larkin 1977). When predators in a western Canada stream were destroyed, survival of fry was much higher (Lack 1954). The only density-dependent aspect of predation on fry takes place after fry establish feeding territories. At high densities (sometimes due to low water levels), fry unable to establish territories are displaced downstream and may be consumed by predators (Larkin 1977). Adult salmon in the ocean are preyed upon by sharks, seals, and killer whales, and of course by man in the sea and rivers, but predation on adult salmon has not been demonstrated to be density-dependent (Larkin 1977).

Cannibalism

Many stocks of pink salmon exhibit alternate-year cycles of numerical dominance. Since nearly all Pacific Coast pink salmon spawn at age 2, either the odd-year spawning line is more abundant than the even-year spawners, or vice versa. One mechanism suggested for perpetuating the dominance of one line is cannibalism. Age-0 pink salmon may be abundant in coastal waters at the time the piscivorous age-1+ pink salmon pass through on their way to spawning streams. However, there is no evidence that the older fish alter their feeding habits according to abundance of the younger fish; therefore cannibalism of pink salmon is probably compensatory (Ricker 1962). Sockeye salmon may remain in fresh water for several years (Foerster 1968), thus are potentially cannibalistic, but this is not a documented form of compensation for them.

Competition and Growth

Young salmon of some species establish feeding territories during stream residence and competition for food becomes a density-dependent influence on growth. Young pink salmon survived better at low than high densities, believed due to food competition (Pritchard 1948 cited in Lack 1954).

Young sockeye salmon inhabit lakes rather than establishing stream territories. Some studies suggest that food abundance (zooplankton) influences growth rate of sockeye, but analysis is complicated by increased survival; more fish are present to take advantage of the favorable food supply (Johnson 1965). Rock slides and continuous heavy fishing severely reduced sockeye salmon populations in the Fraser and Skeena Rivers. Subsequently the abundance of young salmon was very low, but they apparently did not grow at an increased rate, nor did competitor fish populations increase noticeably (Foerster 1968). Thus compensation after the catastrophe was not demonstrated.

Coho and chinook salmon reared in Happy Valley Reservoir, Oregon, experienced catastrophic mortalities due to rotenone and subsequently poor water quality which decreased their condition, making them easy prey for the surviving older salmon. Both species displayed density-dependent growth in length and condition after the mortalities, shown by comparing growth rates before and after rotenoning. Also, the first year class after the rotenone treatment grew faster in its first year than the next year class, at least partially due to the difference in fish density between the 2 years (Higley and Bond 1973).

Juvenile coho salmon in a limited-food laboratory experiment grew faster in the absence of juvenile steelhead trout (*Salmo gairdneri*), given the same food ration and total fish densities (Laarman 1969), indicating steelhead trout have a competitive advantage over coho. Kokanee salmon (landlocked sockeye) grew faster in Kootenay Lake after introduction of mysids, and while eutrophication was proceeding (Northcote 1972).

There is some evidence for density-dependent growth of salmon during their life at sea. Seven sockeye salmon stocks showed significant decreases in growth rate, up to 10-22% for two stocks, when large numbers were present. The most noticeable effects were early in ocean life and were believed to be due to competition for food. Total sockeye abundance in the Gulf of Alaska was at least as important as within-stock abundance in determining body size (Peterman 1984). Increased food abundance in the ocean contributes to faster growth of sockeye (Foerster 1968). Other salmon species apparently have not shown density-dependent growth at sea. Abundance of juvenile migrants may be associated with smaller size of returning adults, but the evidence is conflicting (Larkin 1977).

Mortality at sea is less when smolt size is larger (Larkin 1977), thus density-dependent growth in streams may help determine later mortality of fish. Similarly, high rates of marine mortality for sockeye (probably due to predation) are associated with large smolt productions, suggesting a density-dependent response (Larkin 1977). For pink salmon, however, mortality at sea does not appear to be compensatory over the range of observed population sizes (Larkin 1977). When Snake River chinook salmon juveniles were greatly reduced in abundance by dam effects, record-low numbers of adults returned in spawning runs (Raymond 1979). This demonstrates a lack of compensation during sea life; mortality was not density-dependent.

Age at Maturity

Fast-growing sockeye salmon migrate to sea 1 year before slower-growing ones; also, faster-growing sockeye mature and return to spawn sooner. The range for age at spawning is 3 to 8 years (Foerster 1968). Heredity, however, exerts more influence on age at maturity than environmental (i.e., food) factors.

Fecundity

Fecundity of sockeye salmon increases with size (Johnson 1965), thus density-dependent growth would result in higher fecundity. However, the range in size and thus egg production in south Kamchatka was within 12-18% of the mean over long periods of time (Krogus 1961 cited in Johnson 1965), thus fecundity would not be a strong population regulator. Other populations of sockeye have demonstrated no density-dependent effect on fecundity (Johnson 1965).

Summary

Density-dependent incubation mortality related to spawning site competition, and density-dependent juvenile growth and survival due to (usually) intraspecific competition for food, appear to be important compensatory mechanisms for Pacific salmon. There is also some evidence for compensatory egg deposition, age at maturity, and under certain conditions,

fecundity and predation. Cannibalism is prevented for some species by the spatial separation of young and adults, and in the species where it does occur, it may not be compensatory.

RAINBOW SMELT

Introduction

The smelts (Osmeridae) are anadromous fishes having an irregular but wide geographical distribution throughout the Northern Hemisphere (Kendall 1927). The rainbow smelt, *Osmerus mordax* (Mitchill), is an introduced, landlocked form which is common in the Great Lakes. Regier et al. (1969) believed Lake Erie smelt populations had relatively good self-regulating mechanisms, preventing wide fluctuations in abundance.

The following information concerning rainbow smelt of western Lake Superior is provided in a study by Bailey (1969): (a) The growth rate of smelt was variable; a large range of lengths for fish in each age-group resulted in length being a poor index of age. (b) Female smelt were found to grow faster than males after the second year. (c) Both sexes made their best annual growth in length during their second year of life; largest weight increases came in their third year. (d) All 1-year-old smelt were immature; whereas, for 2-year-old fish 40.7% of the males and 17.7% of the females were mature; all smelt greater than 2 years old were mature. (e) No smelt less than 127 mm were mature but all individuals in the 150-155 mm length interval were mature. (f) Spawning males were generally shorter than spawning females and average length of both sexes decreased as the spawning season progressed. (g) The sex ratio and mean age of spawning-run smelt also varied according to the time within the spawning season. (h) Males dominated the spawning populations at the start of the run, the sex ratio was near 50:50 at the peak, and females may have been dominant as the spawning season closed. (i) Fishermen generally began to harvest smelt at the beginning of the spawning season and fishing effort declined with time as markets and appetites became glutted; as such, the males which initiated the spawning run suffered greater mortality than females; males were not caught beyond age-group 5 and females strongly dominated age-groups 4-7. (j) The average number of eggs contained in the ovaries of 10 smelt between 185 and 224 mm was 31,338.

Community Interactions

Present-day rainbow smelt stocks in the Great Lakes resulted from the planting of over 16 million eggs in Crystal Lake, Benzie County, Michigan, in April 1912 (Van Oosten 1937b). Smelt spread progressively from Crystal Lake to all of the Great Lakes, but this process was inhibited by time lags involved in locating suitable habitats (large bays of shallow-to-moderate depth) in the lakes, and due to resistance to colonization in the form of predation pressure (Christie 1974). According to Eck and Wells (1983) rainbow smelt comprised 18% of the 3,037 metric tons of forage fish consumed by lake

trout in Lake Michigan from 15 May to 1 December 1979. Christie et al. (1972) reported that offshore predators preyed on adult smelt while predators in the littoral zone ate juvenile smelt. Release from predation pressure resulted from the decline of predator populations (caused by overfishing and lamprey predation) and allowed smelt populations to increase.

Eutrophication of the Great Lakes also may have favored smelt over native species. Apparently eutrophication causes destabilization or shifts in food bases or habitat characteristics such that shifts in species dominance are ongoing. Compared with native species, an invader under unstable situations faces much less organized resistance and has a better chance of succeeding provided it can accommodate to the new environment (Christie et al. 1972). The ability of smelt to accommodate to new environments is illustrated by their flexibility in reproduction requirements. Normally being stream-run spawners, smelt adapted to reproducing on limestone ledges of points (Christie 1972). Also documented is the ability of smelt to compete with or prey on other species. Smelt are widely implicated in the decline of coregonines (Christie 1972, 1974; Christie et al. 1972; Crowder 1980; Wells and McLain 1972) and in particular have been known to prey on lake herring (*Coregonus artedii*) larvae and probably other species (Christie 1972; Selgeby et al. 1978; Crowder 1980). Smelt are not always the superior competitor however; explosions of alewife populations may have caused declines in smelt populations in Lakes Michigan and Huron. The Wisconsin Department of Natural Resources and Wisconsin Electric Power Company have unpublished data on Lake Michigan smelt populations.

Another factor which may relate to the pollution resistance of smelt was reported by Christie (1974). The sessile eggs of smelt rest on short pedicels and as such are free from the bottom where pollution or the effects of pollution may be concentrated.

Mortality Factors

Rainbow smelt in the Great Lakes are fished extensively by both commercial and sport fishermen. It is mainly by these fisheries that the abundance of smelt populations is measured or followed. The commercial fishery consisted mainly of gill nets set under the ice and pound nets. Sportsmen harvest rainbow smelt by using dip nets or shore seines during the spring spawning runs.

Natural fluctuations of rainbow smelt populations occur due to many reasons. Mass mortalities and subsequent recoveries of rainbow smelt populations have been cited in the literature, but most such occurrences seem poorly understood, and did not have follow-up studies. Kendall (1927) reported on the sudden simultaneous deaths of thousands of rainbow smelt in Lake Champlain both in 1882 and 1883. These mortalities were attributed to various phenomena including the aurora borealis, electric storms, and windstorms but no explanation adequately accounted for the die-offs. In Lake Ontario, rainbow smelt stocks declined from 1952 to a low in 1965 but have since recovered substantially (Christie 1972). The decline was thought to

have been related to the amount of spring run-off, but subsequent observations made this hypothesis doubtful, and in any case, other unknown factors were probably involved (Christie 1972).

Compensatory Mechanisms

Growth--

The most massive rainbow smelt mortality occurred in Lakes Huron and Michigan during fall and winter, 1942-1943 (Van Oosten 1947). Because fishery statistics were available from before, during, and after the mortality, we have a good chance to evaluate the compensatory potential of smelt. The mass mortality was attributed to a bacterial or viral disease which killed smelt of all ages and sizes and both sexes, starting in Lake Huron and spreading to Lake Michigan. Just prior to the mortality, fishery statistics indicated that smelt populations were very abundant, perhaps more abundant than ever before. The disease decimated the smelt populations and virtually wiped out the fishery for a few years. The commercial gill net catch dropped 61% and the pound net catch dropped 93% between the 1939-1942 means and the 1943 catch, and catch was almost nil during 1944 (Van Oosten 1947). Some signs of recovery were indicated in 1945, but smelt abundance was thought to have been less than 10% of the "pre-mortality" years. Further recovery was observed in subsequent years and stocks re-attained full abundance in Lake Huron by 1950; recovery was rather slow in Lake Michigan but a high yield was obtained in 1958 (Christie 1974). Compensatory growth of smelt in Green Bay, Lake Michigan, was observed as fish in 1944 and 1945 were significantly longer and heavier than fish of corresponding age captured in the same region in 1941 (Table 10). After the mortality, smelt populations recovered more slowly and fluctuated less than alewife did after their 1967 mortality (Brown 1972; Christie 1974).

Fecundity--

Some evidence for compensatory fecundity of rainbow smelt was reported by Gerking (1976). When a Lake Michigan population of rainbow smelt was subject to impingement by the Zion Power Plant, fecundity per gram body weight increased for fish of all length classes from 140 to 239 mm. The most dramatic difference was shown by 160-169-mm fish, which had mean fecundities of 443 eggs per gram body weight in 1973, 540 eggs/g in 1974 and 927 eggs/g in 1975 (Gerking 1976).

Cannibalism--

Yearling and older rainbow smelt in the Great Lakes region prey on conspecific juveniles, sometimes with greater frequency than they consume other fish species (Creaser 1929; Hale 1960; Gordon 1961; Price 1963; O'Gorman 1974; Great Lakes Res. Div. unpub. data). Although the data do not document increased cannibalism at higher smelt densities, generally cannibalism is likely to be more intense when many young fish of that species are available, thus cannibalism may be compensatory for smelt. Lake Erie rainbow smelt

TABLE 10. Average total length (mm) and weight (g) of pre- (1941) and post-mortality (1944-1945) rainbow smelt from Green Bay, Lake Michigan. Adapted from Van Oosten (1947).

Date	Item	Age-group						
		Males			Females			
		1	2	3	1	2	3	4
Mar 1941	N	0	35	11	1	36	12	1
	len		170	188	135	175	201	193
	wt		28	40	14	31	51	40
Mar 1944	N	2	25	1	1	19	2	0
	len	163	185*	216	160	196*	244	
	wt	28	42*	74	25	54*	96	
Jan 1945	N	1	25	5	2	18	13	2
	len	124	193*	201	140	213**	221*	267
	wt	14	57**	62	17	76**	85*	139

* Significantly greater than pre-mortality ($p < 0.05$).

** Significantly greater than 1944 ($p < 0.01$).

yearlings and YOY are found near the thermocline throughout summer, where cannibalism probably occurs and may have accounted for the alternate-year cycle of abundance observed during the 1960s (Regier et al. 1969).

Summary

Although rainbow smelt populations in the Great Lakes and elsewhere have experienced catastrophic mortalities and recoveries, little attention has been given to the mechanisms of recovery. Smelt from Green Bay, Lake Michigan, compensated after the 1942-1943 mortality by increased growth in length and weight, probably due to decreased intraspecific competition. One study showed fecundity to be compensatory, independently of growth rate. Cannibalism is potentially a strong compensatory mechanism for smelt.

YELLOW PERCH

Introduction

MacLean and Magnuson (1977) state that percids evolved in a simple predator-prey complex in North America. Predation, competition, and other species interactions cause resource partitioning in fish communities which decreases species interactions. The cool-water niche of percids separates them spatially from stenotherms and eurytherms.

Yellow perch (*Perca flavescens*) and Eurasian perch (*P. fluviatilis*) combined have an almost circumpolar distribution in fresh waters of the northern hemisphere. They have been one of the most intensely studied freshwater species because of their importance to sport and commercial fisheries. Yellow perch inhabit waters of moderate temperatures from large lakes to ponds or quiet rivers, and reach greatest abundance in fertile waters with large plankton blooms and rich bottom fauna. They inhabit dystrophic waters where stunting is common (Deelder 1951) to oligotrophic lakes, where they effectively compete with salmonids for available food (Fraser 1978). In more favorable habitats, populations of yellow perch are usually very stable, if they are not undergoing some severe stress, such as overexploitation, competition from an exotic species, or pollution. In most populations, yellow perch maintain their stability through the dual regulatory mechanisms of cannibalism and predation. Among density-independent factors, water temperature at the time of hatching and early recruitment has been consistently cited as important in determining year-class strength. This species has great potential for contributing to our understanding of compensatory mechanisms because of the vast amount of research that has been done and the extensive data sets that exist. Future research can build on the conceptual foundation that already exists for many of the life processes of this species.

We found examples of a large number of different agents which sometimes acted catastrophically to severely depress yellow perch populations. Disease caused a 98% reduction in Eurasian perch in Lake Windermere, and a severe reduction was also recorded for Lake Mendota yellow perch; compensatory increases in growth and fecundity were noted. A die-off of yellow perch in Lake Norman, North Carolina during summer was also noted (J.R. Siler, Duke Power Co., Huntersville, N.C., pers. comm.). Man was responsible for the removal of large proportions of the perch populations in Lake Windermere (Bagenal 1970; Craig 1980) for use during the war, and overfishing reduced populations to low levels in Saginaw Bay, Lake Huron (Eshenroder 1977). Predation by alewife on larval yellow perch was hypothesized by Wells (1977) and Jude and Tesar (1985) to have depressed yellow perch stocks in Lake Michigan. Predation by walleyes in Oneida Lake acted as the agent of compensatory mortality for YOY yellow perch (Forney 1971). The response of yellow perch to changes in competing species (rough fish removal operations - Grice 1957; Johnson 1977) was also studied. The impact of major changes in the environment, such as acidification and eutrophication, will also be discussed so that specific incidences of catastrophic declines can be

understood in reference to the quality of the environment for yellow perch. Clady (1976) has established for Oneida Lake that a series of minor factors, rather than one catastrophic event, established the strength of the final YOY cohort produced. More detail is given under each of the sections to follow.

Growth

Many of the mechanisms of compensation are eventually manifested in growth by fish. Growth is also much easier to measure than, for example, competition. Thus, this section contains many examples of changes in growth which were caused by several different mechanisms. If growth was the dominant response, we report it here.

LeCren et al. (1977) studied the numbers, weight, and year-class strength of Eurasian perch in Lake Windermere, England during 1941-1966. They removed large numbers of yellow perch and northern pike (*Esox lucius*) in an effort to reduce competition and predation on salmonids in the lake. Eurasian perch did not exhibit growth increases in the first few years subsequent to harvesting (Craig 1980). Lack of compensation by the perch population was attributed to (1) Eurasian perch were also intensively harvested, and (2) competing species occupied the "niche" of the depressed perch. An exceptional combination of events, both physical and biological, was necessary before Eurasian perch were able to produce a strong year class. Holling's (1973) concept of "domains of attraction" may apply here, as perch declined from a high population and some equilibrium status with its predator (northern pike) and competitors in Lake Windermere, to a lowered state where populations remained depressed from 1941 to 1955, before a strong year class was formed.

In Lake Windermere, cannibalism by the 1955 cohort caused increased mortality for the 1959 cohort in the south basin (LeCren et al. 1977). Northern pike predation and perch cannibalism regulated populations through the 1960s and 1970s. Northern pike were able to keep the perch populations depressed because perch were already low from the war fishery. To form a successful year class in Windermere, several favorable events needed to occur. Removal of perch through trapping caused a decline in the average age of the fish and a three-fold increase in the mean weight of the perch. This was translated into a three-fold increase in fecundity. The population in 1956 was 6% of the 1941 level so there was only a partial compensation in numbers for the decline. More perch (over two times more) fed on fish in later years (1956) than in earlier years. LeCren (1958) also found that removal of old perch via traps had no effect on YOY and yearling growth since these fish ate zooplankton, while larger fish ate benthos and fish.

Food eaten by Eurasian perch in Windermere showed that adults normally did not eat many YOY perch. However, LeCren et al. (1977) found that culling of northern pike from the lake was very important, since normally northern pike ate age-2+ Eurasian perch, but when this size perch was scarce they switched to YOY and yearlings. Mergansers in Lake Windermere also ate large quantities (up to 3.6 tonnes/year). These predators consorted to depress perch populations so that a good year class was not formed for 13 years (1955)

after the initial reduction of perch and northern pike in 1941. There was an interesting effect of ice cover in Lake Windermere on populations of Eurasian perch. During 1947 and 1963, years of prolonged ice cover, there was a failure of the year class when females failed to spawn. Year-class strength was positively correlated with: (1) warm years, and (2) low biomass of perch present, and negatively correlated with: (1) low temperatures, (2) increased biomass of perch, (3) low ratio of spawning males to females, (4) northern pike predation, (5) merganser predation, and (6) extended period of ice cover. They concluded that the 1941 removal of perch and northern pike from Windermere caused both species to remain in a depressed state despite removal of the fishing pressure. In the north basin, there was a more drastic perch removal and northern pike predation was more severe. As a result, numbers of perch continued to fall. The first good year class was formed in 1959, some 18 years after the first removals of Eurasian perch. In the south basin, fewer perch were removed, northern pike predation was less, and a strong year class was formed much earlier (in 1949, and a very strong one in 1955) than in the north basin where predation was much higher and populations of perch more depressed. Weather was particularly important, since years of warm water temperature were associated with strong year classes.

Grice (1959) found that yellow perch exhibited compensatory growth increases after severe reduction in competing species in a study of Massachusetts ponds. Rapid growth was attributed to reduced competition for food because of lower population densities. A similar response was observed in renovation of Lake Okoboji, Iowa in 1940-1951 (Rose and Moen 1952).

In Oneida Lake during 1965-1971, cannibalism was not decisive in limiting yellow perch year-class strength (Tarby 1974). Bagenal (1982) noted that Eurasian perch in Lake Windermere produced a large cohort in 1955 and cannibalism, along with pike predation, combined to suppress other cohorts. In Oneida Lake, year classes of yellow perch which were most abundant as young often fared poorly as yearlings (Forney 1980). This within-cohort compensatory mortality was probably a consequence of density-dependent growth mediated by changes in zooplankton composition. Alm (1946) put Eurasian perch into perch-free lakes and into lakes with an established perch population; he found that those in the perch-free environment grew much faster. Alm (1952) also showed that cannibalism could suppress recruitment in small lakes where perch was the only species. Pond studies of yellow perch without competing species showed growth of young perch was compensatory (Schneider 1973). These ponds were fertile (higher survival rates) and without perch predators, and contrast with more natural diverse systems (Oneida Lake - Forney 1971) where predation was the principal mortality factor, and it was often compensatory. Schneider concluded that extrinsic mechanisms, such as predation or competition by other species, were necessary to stabilize perch populations so large fish are produced.

Overfishing removes large proportions of the adult population of yellow perch and is another category of catastrophic loss. Spangler et al. (1977) discussed the impact of overfishing on Great Lakes stocks and found there were typical responses, such as changes in variability of recruitment, compensatory increases in growth rate, and reductions in age of first spawning. Forney

(1971) with walleye in Oneida Lake and Schmitz and Hetfeld (1965) with muskellunge (*Esox masquinongy*) in a Wisconsin lake both showed that predation removed enough yellow perch from the population to cause compensatory mortality and increased growth of remaining perch.

Sometimes density-independent processes can impact yellow perch year-class strength. Clady (1976) found wind was negatively correlated with early survival, which varied from 1.6-18.4%. Physical destruction of eggs and greater mortality of prolarvae in low temperatures were cited to account for low survival during some years. However, he felt a number of minor mortality factors, rather than a catastrophic event, controlled survival. Another environmental change, gradual acidification (Beamish 1976; Ryan and Harvey 1980), caused yellow perch to first lose competitors, then as perch populations became increasingly stressed, reduced densities of age-groups 1-3 occurred; survivors responded with increased growth. Older fish had high mortality and severe osmotic stress.

Environment also impacts yellow perch and their compensatory response. For example, in Lake Memphremagog, Quebec, two basins, one enriched and the other not, had perch populations which grew at the same rate, but more were produced in the enriched one. Here, since perch were growing near maxima for the species, the increased energy was channeled into increased numbers, rather than increased growth. Kelso and Bagenal (1977) in their treatise on unperturbed systems, stated these environments were harsh and perch there were characterized by low growth and variable to low recruitment. An infestation of Eurasian milfoil (Borawa et al. 1978) favored yellow perch which had increased populations to the detriment of some other species. Finally, Leach et al. (1977), studying the response of percids to eutrophication, found they generally benefit since competitors and predators are less tolerant and food supply increases.

In other studies, Wells (1977) addressed the changes in yellow perch populations in Lake Michigan. He found that yellow perch declined abruptly in the mid-1960s about the same time as the alewife invasion. The commercial fishery also hastened the decline. Reduced densities of yellow perch allowed increased growth, which resulted in the commercial fishery increasing their harvest even more. After the alewife die-off in 1967, yellow perch populations increased, but this was only a small effect. Recent papers (Wells 1985; Jude and Tesar 1985) document a sharp decline in the numbers of alewife in Lake Michigan, which was predicted by Stewart et al. (1981). They warned of this decline because of the increased stocking of salmonids. In response to the alewife decline, yellow perch populations have increased dramatically, which was hypothesized by Wells (1977) to occur because of reduced predation by alewife on yellow perch larvae. Wells (1985) chronicled this yellow perch expansion in more recent years and found the 1983 year class was probably the largest ever produced in Lake Michigan. In addition, a decline in growth of yellow perch was recorded as populations apparently hit their peak and food became limiting. Yellow perch of the 1983 year class reached an average total length in the southeastern part of the lake of only 100 mm at the end of 2

years; in the 1970s this length was about 160 mm. By weight, these same fish produced in the 1970s were four times heavier than those produced in 1983 after 2 years of growth.

Leach and Nepszy (1976) examined yellow perch trends in Lake Erie. They found that large year classes of yellow perch and walleye were produced in 1959, 1962, 1965, and 1970 which were strongly related to water temperature. They noticed no major growth rate changes since the 1950s. Yellow perch was the dominant percid in catches from Lake Erie in the 1970s.

Nelson and Walburg (1977) found that growth of yellow perch in their first summer in two Missouri reservoirs was inversely proportional to abundance. Mills and Forney (1981) found that since 1968, YOY yellow perch growth in Oneida Lake was inversely correlated with density. An increased density of YOY caused the main food (*Daphnia*) to decline which in turn acted as a mechanism to depress YOY numbers, presumably through increased starvation. Density-dependent growth was mediated by *Daphnia* populations and year-class strength. Schmitz and Hetfeld (1965) studied muskellunge predation in a Wisconsin lake and found that muskellunge ate mostly yellow perch > 150 mm which reduced yellow perch densities and resulted in increased growth for age-1 and 2 yellow perch. A growth increase was not observed for YOY because they ate zooplankton.

Competition is suspected to be an important compensatory mechanism, but it is difficult to quantify. In a study on yellow perch in Wilson Lake, Minnesota, Johnson (1977) found that yellow perch and white sucker (*Catostomus commersoni*) were competing for the same resource. Abundance, growth rate, and condition factor of yellow perch increased after 85% of the weight of the white sucker standing crop was removed. Yellow perch numbers then increased, and density-dependent mechanisms (probably food limitation) operated to cause growth and condition of yellow perch to decline in later years.

Fraser (1978) studied the impact of the introduction of yellow perch into oligotrophic lakes stocked with three species of salmonids. In 1962 only salmonids (brook trout, *Salvelinus fontinalis*; splake, *S. fontinalis* x *namaycush*; and rainbow trout, *Salmo gairdneri*) were stocked in the lake. Yellow perch entered in 1967 and showed an immediate burst of growth. Thereafter, the yellow perch population increased drastically and their growth declined. Salmonid production and growth declined and food eaten by salmonids shifted to smaller items. Both inter- and intraspecific competition occurred.

Similar consequences were observed by Alm (1946) who studied stunted perch in Swedish lakes. A natural reduction in perch resulted in increased growth rates. Removal of Eurasian perch from Lake Windermere also caused the growth rate of remaining fish to increase (Bagenal 1970). In general, a decline in the numbers of yellow perch results in increased growth of adults (Rutledge and Barron 1972). Thorpe (1977), in an effort to study stunted yellow perch populations, found that with increased food, *Gambusia*, growth also increased.

Kelso and Bagenal (1977) reviewed percids in unperturbed ecosystems. Growth in these lakes was low, and recruitment was not regular, because these systems were usually in harsh environments. Temperature stood out as a major controlling factor. They felt that genetic factors did not constrain yellow perch growth, since fish could be transplanted from these harsh systems and grow well in a favorable environment. They concluded that these systems had low productivity and that stability of biomass appeared to exist for yellow perch.

Alm (1946) noted that strong year classes restricted recruitment through cannibalism while the age-group was passing through the population. Craig (1980) noted this effect for the 1955 cohort of Lake Windermere Eurasian perch. This mechanism appears to exist for yellow perch.

Ryan and Harvey (1980) studied the response of yellow perch in acid lakes in Ontario. Yellow perch in these lakes generally had low population densities; those of age 1-3 showed increased growth, while fish of age 4-9 had depressed growth. They concluded that yellow perch growth may serve as an indicator of environmental stress. There was less successful recruitment of yellow perch in more acid lakes. The mechanisms proposed to explain the increased growth of age 1-3 fish were less inter- and intraspecific competition because of lowered densities of yellow perch in these lakes. Those fish greater than 3 years old had depressed growth, which was due to increased maintenance costs for older fish in the acid medium. This osmotic stress was due to loss of sodium. In addition, there was less prey available to older fish, as the acid-intolerant groups such as minnows declined.

El-Zarka (1959) examined the Saginaw Bay yellow perch fishery and found that growth declined in 1943-55 compared with 1929-30 growth rates. He concluded that the growth decline in the 1940s was due to a lack of space because, he concluded, there was plenty of food. The mean age in trap net catches increased from 3.8 years in 1929 to 4.3 years in 1955 and as well, growth decreased. Modal length declined from 8.5-8.9 to 6.5-6.9 inches. Sexual maturity occurred at a smaller size in 1955; females were mature at 5-7.5 inches, while males matured at 7-7.4 inches.

Ricker (1963), in his paper on big effects from small causes, pointed out that a 5% increase in catch can cause a 12-15 age-group stock to decline. These stocks depend on having a large number of multiple age-groups eligible to spawn to overcome the vagaries of the weather and other physical factors that can adversely affect stocks. A population that produces greatest sustained yield at 75% is close to the knife edge, and if use increases it may collapse. We saw examples of this with the Saginaw Bay fishery, where exploitation reduced the larger females to the point that recruitment failure resulted (Eshenroder 1977). Similar effects were noted for Lake Erie (Nepszy 1977).

Age at Maturity

Spangler et al. (1977), in a review paper on percids, concluded that percids in response to exploitation exhibited a change in the variability of recruitment, increased growth rate, and a decline in age at maturity. Less tractable changes included changes in the genetic stock and changes in interspecific relationships. Changes in genetic stocks due to overfishing were not documented, but must have occurred in the fishing-up process. These types of changes, especially early reproduction, can be deleterious, since as Roff (1984) pointed out, reproduction can cause decreased growth or an increase in mortality. Therefore populations that are impacted so that there is a decrease in the age at maturity may experience early mortality as an additional effect. Yellow perch in Lake Erie have also exhibited a decline in age at maturity as the time of first spawning went from age 3 in 1927-1937 (Jobes 1952) to age 2 during more intense exploitation in 1960-1966 (Spangler et al. 1977).

In Lake Windermere, Craig et al. (1979) found that, after the die-off that killed 98% of the perch, age at maturity declined. Eurasian perch in 1978 matured at age 2; whereas, before the die-off they matured at age 3. This was due to increased food per fish which resulted in increased growth and reproduction.

Sex Ratio

Eshenroder (1977), studying the effects of several factors on the yellow perch of Saginaw Bay, Lake Huron, found as fishing pressure increased in Saginaw Bay there was an increase in growth rate, a decline in the average age in the catch, females became scarce because they grew faster and were harvested earlier than males, and these changes resulted in low recruitment because of low brood stock. Temperature was important in determining year-class strength. In 1966, the size limit on the commercial fishery was removed, more fish were harvested, and immediately there was an increased growth rate in remaining perch, a shift toward younger fish, and a decline in the abundance of female spawners. Trawl samples revealed that only 11% of the catch was female, a shift in the sex ratio that had significant ramifications for recruitment. A decline in the walleye populations in the 1940s and an increase in the numbers of alewives and rainbow smelt affected the abundance of yellow perch the most. Walleye restrained yellow perch populations through predation, allowing good growth; when walleyes declined, yellow perch numbers increased. Males were more abundant (62%) in Saginaw Bay in 1955, at high population levels, than in 1929 (25%), at low abundance (El-Zarka 1959).

In 1941, the year removals were initiated in Lake Windermere, the sex ratio was two males to one female and the male Eurasian perch biomass was 1.25 times the female biomass (LeCren et al. 1977). In 1944, after removals, the ratio was 0.7 males per female and the male biomass was also reduced to 0.17-0.26 times the female biomass.

Predation

Forney (1971) showed that compensatory mortality can occur in yellow perch populations in Oneida Lake. From trawl catches he found that there was a decline in catch from August to October which was more severe for weak than strong year classes. The decline was due to walleyes which ate a fixed number of prey items regardless of the size of the yellow perch population. Nepszky (1977) has concluded from studies of Lake Erie yellow perch that increased exploitation has caused irregular recruitment and no strong year classes were formed. Predation on yellow perch by rainbow smelt and walleye was cited as a possible contributing factor.

Lawler (1965) studied Hemming Lake in Ontario and removed a large quantity of northern pike. The density of yellow perch immediately increased. In Oneida Lake, New York, YOY yellow perch are preyed on by walleyes which have a stable population and are usually the main determinants of year-class strength in yellow perch (Forney 1971). In Windermere, Eurasian perch are preyed on through age 4 by northern pike and the predator population is unstable.

Cannibalism

Eschmeyer (1936) recorded some of the characteristics of stunted yellow perch populations in northern Michigan inland lakes. He found that stunted fish preyed heavily on YOY and yearlings and that older fish died of starvation. Most fish were 2-year-old fish. Stunted fish grew slowly; 75% were age 2 and the sex ratio was 74 females to 100 males. Most females were older fish and the young fish were males; smaller fish ate insects, while older fish starved to death. Tarby (1974), in studies of Oneida Lake yellow perch, found them to be cannibalistic. However, during the period of study the growth rate of young perch appeared independent of density. This finding suggests that cannibalism was unrelated to perch abundance (density-independent). In fact, Forney (1971) found that during their first year, young perch experienced compensatory mortality, which was attributed to walleye predation.

In a related paper, Smyly (1952) found yellow perch fry were cannibalistic when the zooplankton crop was depleted in June-August; however the effect on the populations was undetermined. Ilina (1973, cited in Spangler et al. 1977), in experiments in Russia, showed how some density-dependent mechanisms worked for perch. The proportions of cannibals (YOY) varied according to the environment. There were usually three groups of YOY perch that formed, given a starting group of all the same size and age. This included a group that ate plankton, one that ate benthos, and one that was cannibalistic. When the temperatures under which the experiment was conducted were cool and within a narrow range, few cannibals resulted. However when the water was warm, fish grew faster, and more cannibals were produced.

A generalization about yellow perch seemed to emerge from the studies examined. When yellow perch were studied in ponds or lakes where they were the only species present, cannibalism acted as a strong density-dependent regulator of the populations (Alm 1946; Schneider 1973). In contrast, in more diverse systems with stable predator-prey systems, predation was the most important agent regulating perch populations, and cannibalism was density-independent (Forney 1971; Craig 1980).

Interference Competition

Ricker and Gottschalk (1940) studied the impact of the removal of rough fish from Bass Lake, Indiana. They removed 40 metric tons of common carp, 18 metric tons of carpsuckers (*Carpiodes* spp.), and 5 metric tons of buffalos (*Ictiobus* spp.). Their removal caused the abundance of game fish including yellow perch to increase. Borawa et al. (1978) studied the fish populations of a lake before and after an infestation of Eurasian milfoil in Currituck Sound, North Carolina. After the invasion, yellow perch and ictalurids increased the most.

MacLean and Magnuson (1977) found that predation and competition were the most important driving forces within *Perca* and in their interactions with other species as well. Percids are temperate-zone mesotherms and are usually spatially segregated from other fish. Thus species interactions are minimized with regard to food and temperature because of their segregation from other species. Predation is intense on and by yellow perch. Interaction with other species is a major complicating feature in diverse ecosystems, and is no less so for yellow perch.

Yellow perch have been impacted by exotics and competitors and in turn have acted as strong competitors. There is ample literature discussing the impact of alewife on yellow perch populations in the Great Lakes and in inland lakes (Kohler and Ney 1980). Wells (1977) discussed the impact of alewife on Lake Michigan yellow perch, populations of which were severely depressed. Predation by alewife on perch larvae was the probable cause. Eshenroder (1977) discussed a similar pattern for yellow perch in Saginaw Bay, Lake Huron, but overfishing and walleye population changes were also important agents of change. In fact he argued that populations of rainbow smelt and alewife were high during periods of abundance of yellow perch. The major difference between the Lake Michigan and Saginaw Bay cases may be the abundant vegetation and large tributaries running into the bay which may have provided refugia for larval yellow perch until they grew large enough to escape alewife predation and competition.

Changes in dominance of the rudd (*Scardinius erythrophthalmus*) and roach (*Rutilus rutilus*) in an English lake (Burrough et al. 1979) provide another example of the depressing influence of a competing species. Competition for food at early life stages was the cause for low Eurasian perch survival in the presence of high populations of roach (Burrough et al. 1979). In Wilson Lake, Minnesota, white suckers were removed, which resulted in a concomitant increase in yellow perch growth (Johnson 1977). The reverse case occurred

when yellow perch were inadvertently introduced into oligotrophic lakes stocked with salmonids - salmonid growth declined and yellow perch numbers and biomass increased dramatically (Fraser 1978).

Acidification of lakes also provides another interesting sequence of events involving the very insensitive yellow perch, and provides more insight into the impact of competing species on yellow perch and compensatory responses to release of this pressure. Beamish (1976) and Ryan and Harvey (1980) presented a hypothesis backed with strong evidence and literature on how fish respond to increasing acidification of lake habitat. As a lake increases in acidity, a pattern of loss of competing species occurs, which favors yellow perch growth and survival. Then, under severe acid conditions, good growth of younger age-groups (1-3) is observed, but older fish (>3) experience physiological stress and starvation.

Starvation

Deelder (1951) studied stunted yellow perch in Holland. Yellow perch exhibited good growth to 14 cm, then there was no growth. Eschmeyer (1936) also examined stunting in Michigan lakes and also found little growth by larger individuals. Both investigators attributed this to starvation of these larger fish which had inadequate prey. Alm (1946) also found similar patterns in the stunted fish he studied in Sweden. Some populations grew very little but lived for unusually long periods of time, up to 18 years.

Stress

Clady (1976) studied the importance of catastrophic events on yellow perch eggs and larvae in Oneida Lake. He found that survival from the egg to the larval stage was 1.6 to 18.4% and that survival was positively correlated with temperature and negatively with wind. Year-class size was determined by a complex of minor factors rather than by catastrophic events. Low temperature adversely affected prolarval yellow perch.

Eshenroder (1977) found that the decline of yellow perch in Saginaw Bay was related to eutrophication. Changes which occurred in response to increased eutrophication included: (1) switch to alternate prey, (2) change in distribution when the environment was degraded, and (3) reproductive behavior adaptations. Eutrophication affected the selection and succession of species.

Disease

Craig et al. (1979) reported on a disease that impacted the Eurasian perch of Lake Windermere. Disease killed 98% of the yellow perch in 1976. Fungus and epidermal lesions were noted on fish in January 1976; in September 1976 all attempts to catch adult yellow perch failed. This resulted in increased fecundity (almost fourfold) as remaining fish compensated for the

loss of most of the population. For example, from 1944 to 1960, fecundity stayed about the same, 13,000 eggs/fish, but in 1977 after the die-off, fecundity increased to 47,000 eggs/fish. Craig et al. (1979) determined that numbers of perch in the lake prior to wartime harvesting (1941) were considerably higher than populations in 1967 to 1976. However, biomass values were very similar between the two time periods indicating the population was at a high level and was trying to achieve stability of biomass. The precipitous decline in 1976 due to disease may thus be density related.

Disease has caused catastrophic declines in Lake Mendota yellow perch (Bardach 1951) and Lake Windermere Eurasian perch (Craig et al. 1979). Compensatory increases in growth occurred because of reduced intraspecific competition and cannibalism.

Parasites

Leach et al. (1977) examined the response of yellow perch to eutrophication. Yellow perch have a curve of response to increased eutrophication where production first increases, then declines. The sequence is predictable and can be exacerbated by overfishing and habitat changes. As eutrophication increases, yield of yellow perch may not increase since nutrients sometimes are channeled through unharvested food chains. Yellow perch biomass and growth increase to threshold levels then decline. Parasites increase with increased nutrient enrichment. In Lake Windermere, Eurasian perch showed increased growth due to eutrophication. Parasitism also increased with eutrophication there since the incidence of *Diplostomum* sp., a parasite which causes hematoma of internal organs, increased dramatically and caused an early summer mortality of adults (Craig et al. 1979). Parasites increased because of more vegetation which provided more habitat for snails, intermediate hosts for the parasites.

Summary

A strong characteristic of yellow perch populations is self regulation, which is clearly and abundantly documented for well balanced, and even highly exploited populations. In many cases, cannibalism acts as a coarse control of populations, allowing increased growth of remaining fish and ensuring a greater chance of survival. Predation acts as a fine control on remaining fish, which at times can cause compensatory mortality in YOY (Forney 1971). In Oneida Lake, cannibalism was determined to be density-independent (Tarby 1974) while Alm (1952) found that it was the principal mechanism of establishing dominance in dystrophic lakes, where perch was the dominant species in a low diversity system.

The most catastrophic decline in perch populations occurred in Lake Windermere, England, where over 98% of the Eurasian perch were lost to disease in 1976. This decline prompted compensatory increases in growth, fecundity (fourfold), and a decrease in the age at maturity of these fish. A myxosporidian disease, reduction in a competing species, and increased fishing

pressure on yellow perch in Lake Mendota, Wisconsin caused a reduction in cannibalism on YOY and a compensatory increase in growth in remaining yellow perch (Bardach 1951). Removal of large numbers of Eurasian perch from Lake Windermere in 1941-1947, to provide food for English people during the war, depressed perch population numbers for many years. Northern pike predation also contributed to depressed perch recruitment.

Predation by walleyes (Forney 1971) and muskellunge (Schmitz and Hetfeld 1965) caused compensatory mortality in yellow perch resulting in increased growth among remaining fish. In another case (Lake Windermere - Craig 1980), removal of Eurasian perch via trap nets did not elicit a compensatory growth increase because perch continued to be cropped off and competing species occupied the "niche" of the yellow perch. Predation also entered into Lake Michigan yellow perch-alewife interactions. Wells (1977, 1985) and Jude and Tesar (1985) postulated that alewife eat the larvae of yellow perch, thus reducing their population levels. An alewife die-off in 1967 and a collapse in the alewife population in 1982 have resulted in an immediate resurgence of the yellow perch population, first by increasing abundance. The most recent collapse of alewife allowed yellow perch to reach a peak in 1983, and reduced growth resulted as density-dependent processes apparently took effect.

Competition, though difficult to document, was suspected in the case of the rudd, Eurasian perch, and roach in England. Competition for food at early life stages caused low survival of perch in the presence of high populations of the roach (Burrough et al. 1979). In a comparable case in a Minnesota lake, a competing species, white sucker, was reduced substantially and a concomitant growth increase in yellow perch followed (Johnson 1977).

Overfishing has reduced populations of yellow perch in several lakes (Eshenroder 1977; Spangler et al. 1977). In most cases responses were generalized: changes in variability of recruitment, compensatory increases in growth rate, and a reduction in the age at first spawning.

Some major changes in the environment have provided evidence of compensation in yellow perch populations. Acidification of lakes has generally favored yellow perch survival and growth, since perch are one of the most insensitive species (Beamish 1976; Ryan and Harvey 1980). At a pH of 4.5, good growth of younger age-groups (1-3) occurs, but fish >3 years old experience physiological stress and starvation. Eutrophication generally favors yellow perch (Leach et al. 1977). In the case of Lake Memphremagog, Quebec, there were two different basins, one enriched and the other less so. Perch did not grow faster in the enriched basin, but instead produced higher numbers of fish than in the less productive basin (Nakashima and Leggett 1975). Lastly, Clady (1976) found the pattern of early survival of larval yellow perch was due to a number of minor mortality factors, rather than one catastrophic event.

Nielsen (1980) concluded that there were complex patterns and causes of mortality for yellow perch in Oneida Lake, which were also observed in the Lake Windermere case (LeCren et al. 1977). These interactions indicate that a

simple model cannot explain or predict the response of percids to an altered environment or altered fish community, or forecast the structure of percid communities across broad habitat or geographical ranges.

WALLEYE

Introduction

The distribution of walleye (*Stizostedion vitreum vitreum*) is limited to the fresh waters of North America (Scott and Crossman 1973). This species has been extensively studied and is of great interest to man both as a commercial and sport species.

Factors which have been documented in the literature as having adverse effects on walleye populations may be categorized broadly as: (a) overexploitation, (b) pollution, (c) loss of spawning habitat (destruction of habitat or limitation of access to sites), and (d) climate.

Overexploitation contributed to depletion of stocks of various populations (Carlander 1945; Anthony and Jorgensen 1977), which caused truncation or alteration of age distribution (Busch et al. 1975; Anthony and Jorgensen 1977; Shuter and Koonce 1977), increased growth (Anthony and Jorgensen 1977; Gaboury and Patalas 1984), and decreased CPUE with changes in recruitment to fisheries (Anthony and Jorgensen 1977).

The blue pike (*Stizostedion vitreum glaucum*) of western Lake Erie failed to compensate and became extinct. The primary drain on the population was overfishing, and desegregation through introgression with the walleye (Regier et al. 1969) may have been the ultimate cause of extinction.

Pollution affects walleye populations directly by limiting reproductive success. Construction activity, agricultural runoff, and other factors contributed to long-term ecological changes which affected walleye spawning grounds in Toronto Bay, Lake Ontario (Whillans 1979). Pollution and sedimentation also affected spawning areas in Lake Erie (Busch et al. 1975). In examining effects on fish of acid rain, Beamish (1976) found walleye to be among the more sensitive species; walleye stopped reproducing when pH dropped to around 5.5-6.0.

From the 1950s to the mid-1970s, walleye in western Lake Erie decreased severely in abundance in large part because of loss of suitable spawning habitat (Busch et al. 1975). Walleye numbers were so reduced in the late 1950s that density-dependent processes were not influential and abiotic density-independent factors influenced walleye production. Busch et al. (1975) observed that an uninterrupted series of years with adverse environmental conditions could ultimately destroy the population.

Climate is important mostly as it affects spawning success of walleye. Thermal and wind conditions, water currents, and turbulence are among important climate-related factors noted by Busch et al. (1975).

In Toronto Bay, Lake Ontario, a catastrophic event led to the decline and virtual extinction of a walleye population (Whillans 1979). A protective peninsula was breached by a storm producing unfavorable habitat for walleye and other species. Construction activities and agricultural runoff also contributed to ruination of local walleye spawning grounds at a time when exploitation of walleye was at a peak. Along with long-term ecological changes, these events brought about a decline in the walleye population from which they did not recover. Introgression and appearance of a sterile hybrid were also reported (Whillans 1979).

For this report, information on walleye was gleaned from the literature and organized according to how it related to compensatory mechanisms. Though not always generated from or pertaining directly to catastrophic events, such information as a whole helps define the compensatory potential of walleye.

Growth

Many authors (Wolfert 1969; Johnson 1977; Shuter and Koonce 1977; Colby et al. 1979; Shuter et al. 1979) have recorded an inverse relationship between growth rate and population density. Shuter and Koonce (1977) observed that this relationship for walleye in Lake Erie was somewhat offset by a proportional relationship between growth rate and forage density. Growth rate of Lake Erie walleye increased markedly during the 1950s when the fishery intensified greatly; the average weight of age-3 fish increased from 0.4 kg in 1952 to 1.3 kg in 1960 (Regier et al. 1969). The Lake Erie walleye fishery virtually collapsed in the late 1950s. Comparing 1943-1954 with 1955-1962, average length of walleye in commercial catches increased from 366 to 406 mm, weight from 440 to 731 g, and condition factor from 0.90 to 1.09; simultaneously, average age decreased from 2.7 to 2.0 years. Average length of age-1 walleye in 1958 was 366 mm, whereas the previous high was 348 mm, in 1949. Also, average weights of age-2 walleye, after fluctuating between 294 and 437 g in 1943-1954, increased from 518 g in 1955-1956 to 986 g in 1960 (Parsons 1970). These data demonstrate growth compensation after a catastrophic reduction in density. Forney (1984) however, found that catastrophic mortality of walleye in Chautauqua Lake, New York, did not elicit a detectable increase in growth. In Oneida Lake, New York, growth of certain walleye year classes appeared to have been independent of numerical abundance of an individual year class because competition within a year class was not markedly greater than competition among year classes (Forney 1965).

A study undertaken in Cross Lake, Manitoba revealed that of two discrete walleye populations, the one which was subjected to a higher level of exploitation exhibited a significantly ($P < 0.05$) faster growth rate (Gaboury and Patalas 1984). Comparing data from Lake Nipissing, Ontario during 1967-1968 and 1972-1975, Anthony and Jorgensen (1977) interpreted greater mean lengths of walleye specimens in every age-group recorded during the latter

years as an indication that overfishing had occurred. In Rainy Lake, Ontario, mean total length of age-4 walleye increased significantly from 37.3 cm in 1959 to 41.6 cm in 1965, at the same time as CPUE (expressed in kg of walleye per km of gill net per day) decreased from 32 to 20 (Chevalier 1977). These data show density-dependent growth.

Differences in growth rate according to sex and age of walleye have been documented. Carlander (1945) found that females grew slightly more rapidly than males after the third or fourth year in Lake of the Woods, Minnesota. Females also outgrew males in Oneida Lake, New York according to Forney (1965) who further speculated that growth of YOY and older walleye was probably determined by different factors. Swenson and Smith (1976) indicated that growth compensation by YOY walleye occurs when food availability changes from limited to unrestricted within a growing season.

Implications of different growth rates include earlier maturity of rapidly growing fish, and a relatively high percentage of non-ripening females during years of poor growth (Forney 1965; Colby et al. 1979). Growth was also an important factor in terms of size at maturity (Wolfert 1969), duration of predation and cannibalism on YOY (Forney 1976; Colby et al. 1979), recruitment (Forney 1977), and intraspecific competition (Forney 1974, 1977; Shuter and Koonce 1977). Walleye were more susceptible to angling during years of poor growth when food availability was low (Forney 1965).

Survival

In a study by Forney (1976), survival of walleye from the egg to prolarval stage was very low but consistent; differences in size of year-classes were not attributable to variability in early mortality. Little evidence was found to indicate compensatory mortality during the first year though the possibility existed that it was masked by density-independent mortality. Forney (1984) did not find an immediate improvement in early survival after the catastrophic walleye mortality in Chautauqua Lake. However, reproductive success, probably through improved early survival, increased during the 1940s in Lake Erie while commercial walleye catch was increasing (Regier et al. 1969). According to Busch et al. (1975), reproductive success of walleye in Lake Erie was most clearly related to rates of water warming during spawning and incubation periods.

Abiotic factors which have negative effects on early survival included strong winds, temperature reversals, turbulence, and physical displacement of eggs from reefs to unsuitable mud bottoms (Busch et al. 1975). As for older fish, Colby et al. (1979) noted a tendency for late-maturing walleye to have a longer life span than early maturers.

Forney (1977) related fluctuations in walleye survival with changes in prey abundance. Johnson (1977) proposed that there may have been an initial increase in survival of young walleye immediately following an elimination of white suckers from a lake in Minnesota. Following two extremely weak year

classes, increased survival of walleye (as evidenced by a strong year class) came about in Lake Erie at a time when overall abundance of walleye and other predators was low while forage species abundance was up (Parsons 1971).

Evidence for a relationship between recruitment and relative size of brood stock was conflicting. Shuter and Koonce (1977) found that recruitment increased with increasing numbers of reproductive stock, but Busch et al. (1975) indicated no correlation between the two factors. In Cross Lake, Manitoba, Gaboury and Patalas (1984) studied two distinct walleye populations from two basins. While walleye abundance and catch per unit effort increased in one basin and decreased in the other, survival remained unchanged.

Fecundity

Colby et al. (1979) found that walleye fecundity increased with age, and Wolfert (1969) established that there was a linear relationship between fecundity and weight and between log fecundity and log length, but other factors merit consideration. If low temperatures persist during spawning season and spawning is delayed beyond a certain point, female walleye may resorb their eggs (Busch et al. 1975). In addition, years of relatively low food availability and poor growth translated into higher than normal proportions of non-ripening females (Colby et al. 1979). Forney (1977) inferred that when interspecific competition was great, female walleye matured at small sizes and had small egg complements which, if age at maturity remained the same, would presumably result in a decrease in "r", their intrinsic rate of increase.

Sex Ratio Changes

Based on data for only 1 month of sampling, walleye in Lake of the Woods, Minnesota, exhibited sex ratio changes with age, as males were apparently shorter lived than females (Carlander 1945). The sex ratios (male : female) for various ages were: age 4 = 1.32 : 1, age 5 = 1.11 : 1, and age 6 = 0.64 : 1. Sex ratio was not shown to be density-dependent.

Age and Size at Maturity

Throughout the literature male walleyes were documented as having matured at younger ages and smaller sizes than females (Carlander 1945; Forney 1965; Wolfert 1969; Forney 1976; Anthony and Jorgensen 1977). For exploited populations this may cause problems as females may grow to be recruited into a fishery earlier than males even though females mature at later ages (Anthony and Jorgensen 1977). Mature fish were consistently larger than immatures of the same year class (Forney 1965; Wolfert 1969). When population size decreased, average age at maturity decreased (Shuter and Koonce 1977), and for walleye from Oneida Lake and Lake Erie respectively, Forney (1965) and Wolfert (1969) noted a trend toward earlier maturation among more rapidly growing fish. However, two walleye populations in Cross Lake, Manitoba had different

growth rates but a similar mean age at onset of maturity for both sexes combined (Gaboury and Patalas 1984). Comparing populations from two basins in Lake Erie, Wolfert (1969) found that females from the western basin matured at shorter lengths and younger ages than those from the eastern basin, but males from the western basin matured at longer lengths and greater ages than those from the eastern basin.

Cannibalism

Data from two studies indicated that walleye were not cannibalistic (Swenson and Smith 1976; Johnson 1977) though the former authors recognized that this interpretation may have been invalid due to inadequate sampling. In other studies cannibalism was well documented.

Parsons (1971) found that walleye accounted for 2% of the diet of walleye in Lake Erie, Colby et al. (1979) documented several instances of cannibalism, and the phenomenon in Oneida Lake was studied in depth by Forney (1974, 1976, 1977). According to Forney, intensity and duration of cannibalism acted as a density-independent factor contributing to variation in year class size and as a compensatory factor limiting population size. Because young yellow perch make up the main forage base in this system, they acted as a buffer controlling walleye cannibalism and indirectly regulating walleye population size. Chevalier (1973) inferred from the relative timing of mortality and incidence of cannibalism that cannibalism was the principal source of walleye mortality in Oneida Lake. He speculated that because cannibalism can occur late in the first year of life when most of the mortality has already occurred, cannibalism may be significant in regulating year-class size. Young walleyes in stomachs were significantly smaller than those in trawl catches, suggesting that adult walleyes were selecting the smaller individuals (Chevalier 1973). Cannibalism, like predation, thus may cause growth rates of young fish to appear to increase by removing slower-growing fish.

Disease and Parasitism

Parasites and diseases affecting walleye were tabulated and described by Colby et al. (1979). It was noted that incidence and spread of disease was greater during spawning season when fish were congregated at greater than normal densities.

Predation

By preying on eggs, white suckers were noted as having a potentially large impact on walleye in Lake Nipissing, Ontario; predators on young walleye (northern pike and yellow perch) were thought to have aggravated effects on an already stressed walleye population (Anthony and Jorgensen 1977). Density-independent mortality of walleye during early stages of development has been attributed to factors including predation, inadequate food, or interactions of these variables with climatic factors (Forney 1976).

Predation on walleye may increase during years when poor growth is exhibited by YOY walleye (Colby et al. 1979) or when alternate prey are less available. After the removal of suckers from a lake in Minnesota, the percentage of walleye in the diet of northern pike increased (Johnson 1977).

Some fish have a variety of interactions with walleye on different levels. In the Great Lakes, rainbow smelt preyed on pelagic larval walleye, competed with these larvae for food, but also provided forage for adults (Schneider and Leach 1977). Regier et al. (1969) suggested that abundant rainbow smelt in Lake Erie during the 1950s suppressed or prevented reproduction of walleye and blue pike.

Inter- and Intraspecific Competition

Interspecific competition with walleye was described by several authors. In Lake Winnebago, walleye fry competed for food with freshwater drum (*Aplodinotus grunniens*) fry, and various authors implicated alewife as being serious competitors with walleye fry for food items, or predators on walleye larvae, in northern Green Bay, Lake Michigan, and in Lake Erie (Schneider and Leach 1977; Colby et al. 1979). Removal of suckers from a Minnesota lake allowed walleye YOY to make greater use of small organisms (e.g., crustaceans and small insects) which had been exploited mainly by adult yellow perch but which became more available when these perch switched to more varied diets available after sucker removal (Johnson 1977). Large numbers of common carp, quillback (*Carpoides cyprinus*), and buffalo were removed from Bass Lake, Indiana, over 2 years. Average catch of walleye increased from 2.3 to 5.8 per seine haul over those 2 years (Ricker and Gottschalk 1940), perhaps due to a combination of decreased interspecific competition and improved water quality. In Lake of the Woods, Minnesota, yellow perch and saugers were identified as competitors with walleye (Carlander 1945), and in Lake Nipissing, Ontario, white suckers, northern pike, and yellow perch were competitors with and predators on walleye (Anthony and Jorgensen 1977). Inter-specific competition may affect growth and survival of walleye.

Intraspecific competition can be significant in limiting food availability, food consumption, and growth of walleye (Swenson and Smith 1976), but in most systems both intra- and interspecific competition must be considered. An excellent illustration of this point is provided by Forney (1977) describing Oneida Lake, New York: between 1900 and 1974, a sequence of events led to a decline of American eel and esocids (competitive predators with walleye), and an increase in the walleye population. The mean size of walleye in the lake stayed approximately the same, as the decrease in interspecific competition was apparently balanced by the increase in intraspecific competition. Variability in prey abundance was an important factor in walleye growth and recruitment. Years of high prey abundance enhanced growth of young walleye and reduced cannibalism, favoring development of strong year classes. This led to increased intraspecific competition for food which caused prey abundance and growth rates to decrease, cannibalism to increase, and survival of succeeding year classes to be suppressed. This

scenario repeated over the years adjusted walleye growth to prey production, although time lags and environmental perturbations induced instability in annual growth and recruitment.

Removal of buffalo, common carp, and freshwater drum from East Okoboji Lake, Iowa, did not immediately result in an increase in walleye abundance. However, after a winterkill in the eleventh year of rough fish removal, abundance of YOY walleye suddenly increased from a 10-year average of 10 YOY walleye per seine haul to 196 per haul (Rose and Moen 1952). This increase in recruitment probably reflects improved early survival due to decreases in both inter- and intraspecific competition.

Summary

The walleye does not fluctuate widely in abundance as do some species, e.g., clupeids. However, walleye populations in some areas have suffered catastrophic mortalities from overfishing, pollution, and weather-related causes. Many walleye populations have demonstrated compensation through growth, and both inter- and intraspecific competition operate to control walleye abundance. Survival, age at maturity, cannibalism, and predation are compensatory mechanisms which appear to operate in some populations of walleye and not in other populations. Both predators and cannibals of young walleye have been shown to select the smaller individuals, causing mean growth rate of juveniles to appear faster.

FRESHWATER DRUM

Introduction

The freshwater drum or sheepshead (*Aplodinotus grunniens*) has a large latitudinal range from Hudson Bay south to Guatemala. In the United States it is found from Pennsylvania west through the Great Lakes and Mississippi drainages to Montana and Nebraska (Scott and Crossman 1973). Freshwater drum normally may live up to 13 years with a weight up to 8.2 kg and a length of 750 mm (Wrenn 1968). It is not a favored game or commercial species due to its tough and coarse flesh, especially in larger individuals, although it has been harvested commercially in Lake Erie, Lake Winnebago, and the Mississippi River (Wirth 1958; Butler 1965; Leach and Nepszy 1976).

Catastrophic Mortalities and Compensation Through Recruitment

Only one study reported significant natural mortality to a population of freshwater drum. Dechtiar (1972) noted "considerable" mortality of drum had occurred along with yellow perch in Lake Erie in 1963. This observation was based upon the high numbers of dead fish which appeared along the Ohio and Ontario shorelines during June and July. Some evidence, though not conclusive, for the cause of the kill was a heavy infestation of the protozoan

parasite, *Ichthophthyrus multifiliis*. Although parasitism, which is common for drum (Dechtiar 1972), could be density-dependent, no evidence suggested that this mortality of drum was related to drum density. A rather large yellow perch year class from 1962 may have triggered the parasitic infestation which could have subsequently increased parasitism upon the drum population. Fewer than 5% of the dead fish observed were freshwater drum and no assessment of overall impact on the drum population in Lake Erie in subsequent years was made (Kenneth Muth, U.S. Fish and Wildlife Service, pers. comm.). However, commercial fishing data for Lake Erie (Baldwin et al. 1979) showed no significant change in the total catch of drum caught in 1963 compared to that of previous years. Thus, assuming constant fishing effort in the early 1960s, the mortality of drum in 1963 probably represented a small proportion of the population, at least among larger size fish most susceptible to commercial fishing.

A case of unusually high mortality for drum where some compensatory responses may have occurred was a commercial harvest of drum at Lake Winnebago, Wisconsin between 1955 to 1966 (Priegel 1971). The purpose of this harvest was to control the drum population because it was believed to compete with more desirable game species in the lake. During this operation at least 680,400 kg of drum were removed annually from Lake Winnebago (a 55,772 hectare lake with an average depth of 4.7 meters). The fishing effort was monitored during the study and fish were collected to assess changes in the condition, age, and size composition of the drum population during the harvest period.

Results were that the total catch of drum ranged from 1,540,000 to 2,000,000 kg annually from 1955 to 1959. However, the catch varied from 680,000 to 1,360,000 kg (1,000,000 kg average) from 1960 to 1966. This was said by Priegel (1971) to have indicated a substantial decline in the drum population after 1960. However, his interpretation should be questioned since based on the catch per unit effort data presented for various fishing gear used, no significant change in either the number or biomass of drum taken was evident. The use of catch per unit effort data to interpret a change in a fish population would eliminate bias of the total catch results caused by variable fishing intensity.

The age composition of the Lake Winnebago drum population did change during the commercial harvest period. For example, samples of drum in 1955 and 1960 showed the majority of fish were of age-group 5 or older. By 1963, however, 55% of the drum were in age-group 4 and by 1965 most of the fish were age 1 or 2. Approximately 60% of the fish taken after 1962 were less than 356 mm long whereas in prior years at least 50% of the fish caught were over 356 mm. These results indicated a gradual reduction in the age and size composition of the drum population.

If the overall population numbers and biomass did not change in Lake Winnebago while the percent frequency of smaller and younger drum increased, then the absolute number of younger drum increased. This would indicate an increase in recruitment had taken place. The extent to which numbers of young drum increased in the lake was not clear from this study since the percent frequencies for age- and length-groups given above were not from fish samples

expressed as catch per unit effort. Recruitment apparently increased, although it was not well quantified, and was a density-dependent response to a substantial mortality of the larger freshwater drum, indicating compensation had occurred perhaps as a decrease in mortality of drum larvae. However, the exact compensatory mechanism is not known since no data were obtained on such parameters as larval fish mortality, age or size at maturity, fecundity, or causes of mortality of freshwater drum. We speculate that decreased intraspecific competition allowed improved survival of young drum. An increase in the condition factor of the drum population may have also occurred. However, the condition factor fluctuated over the study period but did not show any consistent increase for any size groups of freshwater drum. Growth rate changes for drum were not analyzed by Priegel (1971).

Large numbers of rough fish, including freshwater drum, were removed by seine and trap from East Okoboji Lake, Iowa. Abundance of drum, both adult and YOY, declined over the 11 years of fish removal, until a winterkill in the last year of the study. Drum YOY had averaged 387 per seine haul in the first 3 years of the removal, then dropped in abundance to 1-3 per haul in years 8 to 10. In year 11, after the winterkill, 217 YOY drum per haul were collected, and YOY of walleye and yellow perch also increased (Rose and Moen 1952). For drum, the increase in recruitment was probably due to decreased interspecific competition. Intraspecific competition was probably not a factor in recruitment success of drum in this case, since numbers of YOY drum had continually declined as drum were removed. Only when other species (e.g., walleye and yellow perch) experienced winterkill were drum able to compensate by increased recruitment, probably through improved early survival.

Potential Compensatory Mechanisms

Various studies have been done with freshwater drum on age frequencies and growth rates in lakes, rivers, and reservoirs (Van Oosten 1937a; Schoffman 1941; Butler and Smith 1949; Daiber 1953; Houser 1960; Swedburg 1965; Wrenn 1968; Priegel 1969). Decreasing latitude and thus generally warmer temperatures apparently accounted for some increase in growth rate of drum (Schoffman 1941; Daiber 1953). A growth response to temperature would be a density-independent phenomenon if temperature alone was a limiting factor. However, as seen in Table 11 where growth rate is compared for various sites arranged from north to south, latitude alone would not account for differences in growth rate. Although food data were lacking for the various studies of freshwater drum, most likely food availability (a potentially density-dependent factor) also would be involved in determining growth rate (Swedburg 1965). The growth of drum also varied with age of the individual, with some populations having the most rapid growth early (Schoffman 1941; Butler and Smith 1949; Nelson 1974) and some late in life (Van Oosten 1937a). The rate of growth appeared to differ only slightly between the sexes (Van Oosten 1937a; Butler and Smith 1949; Nelson 1974). Growth rate variation also had little or no relationship to water level fluctuation in the Mississippi (Butler and Smith 1949) or the Lake Oahe Reservoir on the Missouri River (Nelson 1974).

TABLE 11. Growth and age at maturity for freshwater drum at various locations (arranged in order from north to south). Blank indicates no data.

Location (Reference)	Time Required to Grow to 356 mm	Age Group with Earliest Maturity	Age Group with 100% Maturity
Upper Mississippi (Butler and Smith 1949)	4 - 5 years	2 (males) 4 (females)	6 (males) 7 (females)
Lake Oahe (Nelson 1974)	5 years	4 (males) 4 (females)	6 (males) 7 (females)
Lake Winnebago (Priegel 1969)	6 years	4 (males) 4 (females)	5 (males) 5 (females)
Lewis and Clark Lake (Swedburg and Walburg 1970)	7 years	3 (males) 4 (females)	7 (males) 8 (females)
Lake Erie (Van Oosten 1937a)	5 - 6 years	4 (males) 5 (females)	6 (males) 8 (females)
Oklahoma Lakes (Houser 1960)	2 - 4 years		
Reelfoot Lake (Schoffman 1941)	6 years		
Wheeler Reservoir (Wrenn 1968)	5 - 6 years		

Fecundity of freshwater drum is described as unusually high for fish and would suggest a high resiliency of drum populations to perturbations. Considerable variation in the eggs per female has been noted. Mature females of western Lake Erie contained 43,000 to 508,000 per individual with most having between 200,000 and 400,000 eggs (Daiber 1953). Female drum weighing from 3.6 to 5.9 kg (615 to 734 mm long) in Wheeler Reservoir, Alabama averaged 686,000 eggs (Wrenn 1968). In contrast, females in Lewis and Clark Lake on the Missouri River averaged only 49,300 eggs per fish (Swedburg and Walburg 1970) but were considerably smaller fish than in other areas (0.29 to 0.67 kg) and had a very low growth rate (Table 11). The variation in fecundity for a given population has been related to age but not length or weight of fish (Daiber 1953; Swedburg and Walburg 1970). However, this fecundity relationship to age appeared to hold for only the early years of maturity. No study has attempted to show any density-dependence of fecundity for drum. According to Daiber (1953) only one third of the ova in each female are mature and released in any spawning season (usually May through July). The rest of the ova are held in reserve for the next and succeeding years. Variation in fecundity between study sites (such as between Lewis and Clark Lake and Wheeler Reservoir) was larger than variation within populations and appeared related to growth rate (and thus temperature and probably food availability). Thus, fecundity may depend to some degree on both density-independent and density-dependent responses. However, with such an overall high fecundity of several hundred thousand eggs per female, we are doubtful that differences of even tens of thousands of eggs laid per female in a spawning season would lead to any significant impact on the recovery of drum from a small or catastrophic perturbation. On the other hand, fecundity could be especially depressed, perhaps by a very slow growth rate, as seen for low egg counts at Lewis and Clark Lake (Swedburg and Walburg 1970). In that case, therefore, the ability of the population to respond to a perturbation may be more sensitive to variations in fecundity. However, fluctuations in year-class strength have not been related to fecundity in any study.

The age at maturity of drum varied with location and sex, with males usually spawning at a younger age (Table 11). Early maturity occurred with the fastest growing males (Daiber 1953) and females (Butler and Smith 1949), which was related to a higher growth rate at more southerly latitudes (warmer temperature) (Daiber 1953)--presumably a density-independent response. However, from Table 11, clearly additional factors other than simple temperature would appear to influence the age at maturity since the trend from north to south was not consistent. As mentioned before, growth rate should also be affected by the food availability which might explain additional variation in the age at maturity at various sites. However, no study attempted to show a relationship of age at maturity to food supply which could be a density-dependent response. In addition, Daiber (1953) noted that early maturing females had smaller eggs and suggested this would decrease survival of fish larvae. However, he offered no data on mortality rates of larval fish.

Two studies (Butler 1965; Swedburg and Walburg 1970) attempted to analyze the causes of the observed fluctuations in year-class strength of their respective drum populations. Larger fish appeared to have few predators and

have similar mortality curves for various years despite fluctuations in year-class strength in the Mississippi (Butler 1965). Mortality rates for drum 25 to 84 mm long also appeared independent of year-class strength (Walburg 1971). Furthermore, predation upon eggs and larvae of drum did not appear to be a major source of mortality (Butler 1965). Predation on eggs and larvae should be low since freshwater drum have pelagic eggs and the larvae float at the surface (Daiber 1953). This pelagic characteristic of the eggs probably also would reduce the risk of mortality associated with eutrophication. Butler (1965) finally concluded that year-class fluctuation for the Mississippi drum was almost entirely due to larval fish mortality (i.e., for fish under 25 mm). Swedburg and Walburg (1970) also concluded that larval fish survival determined drum year-class strength at Lewis and Clark Lake on the Missouri River. In the latter case, however, much of the larval fish mortality appeared to be losses of larvae in the discharge of Lewis and Clark Lake dam (up to 10 million larvae in 24 hours), especially at times of high flushing rate (Walburg 1971). However, neither of these studies have estimated natural larval drum mortality rates.

More recently, Cada and Hergenrader (1980) obtained estimates of larval drum mortality rates for fish 5.5 to 11.5 mm long at two locations along the Missouri River in Nebraska for two different years. Based on catch curves for larvae, instantaneous mortality rates ranged from 0.11 to 0.21 per day (mortality rate, Z , is based on the formula $N_t = e^{-Zt}$ where N_t is the frequency of occurrence of fish larvae and t is the age of larva in days). Moreover, the larval fish mortality rates were significantly higher at two stations in 1976 than in 1974, but no reason for such a difference was given. The eventual impact of this variable larval drum mortality rate upon year-class strength was not yet known. Cada and Hergenrader (1980) noted difficulty in estimating mortality of drum larvae smaller than 5.5 mm due to sampling difficulties and problems associated with larval fish drift in the river.

Fluctuations in year-class strength have generally been related to temperature in suspected spawning and nursery areas during June, July, and August. Warmer summer temperatures (measured by cumulative degree days) have been associated with strong year-classes and cold temperatures with weak year-classes (Butler 1965; Swedburg and Walburg 1970). How this would be related to egg and larval fish survival has not been explored. Such a temperature relationship might be indicative of only density-independent regulation of population size if larvae had an intolerance to low temperatures.

Additional work in one reservoir indicated that young-of-the-year drum mortality was high after a drawdown reduced a flood control lake from 1,456 hectares to 283 hectares (Hulsey 1956). However, the drum population data in this drawdown situation were quite variable and not conclusive.

Nothing is documented on the sex ratio or egg deposition for drum and the subsequent effects on production of the species. Since eggs are known to be pelagic, nest building would not occur, and thus competition for spawning sites should be minimal even at high fish densities.

Little predation on adult drum has been described (Scott and Crossman 1973). Predation may be more important for more susceptible young-of-the-year fish, but documentation of this is lacking. The fact that early life history stages float at the surface may effectively limit predation on them in many situations. Butler (1965) noted that several studies observed no drum eggs or larvae in the diet of potential predators.

The effect of disease or parasitism has been discussed only briefly by Dechtiar (1972) for Lake Erie where drum showed high susceptibility to parasites which perhaps led to some mortality in 1963. However, the exact cause of mortality of the drum was never established nor was the parasitism shown related to drum density. Disease and parasitism on drum, especially for young stages of the fish, deserve more attention to explain the suggested mortality during early growth.

Cannibalism has not been described for freshwater drum at all but probably is insignificant as far as adult predation upon their eggs or larvae is concerned. The adults are known to feed mostly at the bottom upon fish and mollusks. Since eggs and young larvae are considered pelagic, they are not likely to be encountered by feeding adults. Thus, even if larval drum mortality was the most important regulator of the population, cannibalism would not appear important.

Interference competition and agonistic behavior also have not been described for drum. However, as a bottom feeder, feeding would be presumably random and thus territorial interactions would be unlikely.

Starvation may have been important in affecting the freshwater drum growth rate in Lewis and Clark Lake (Swedburg 1965), thus producing a lower fecundity, but the effect on mortality was not considered. Variable survival of drum larvae had been related to temperature without supporting data (Butler 1965; Swedburg and Walburg 1970), but temperature could also influence production of zooplankton upon which fish larvae feed. Cold temperatures could decrease food available to the larvae and increase mortality due to starvation--especially at the high densities likely due to high female fecundity. Thus, food availability for drum larvae could be density dependent, but only at cold temperatures.

Mortality from stress also has not been well documented. Cold temperatures may directly stress drum larvae and thus increase their mortality--a density-independent effect. Furthermore, cold temperatures should also slow growth and prolong vulnerable larval fish stages to disease, parasitism, or predation. However, precisely how typical cold temperatures stress drum larvae, if at all, has not been examined.

Summary

Freshwater drum populations appeared to have a high resilience after excessive mortality induced by man or nature. This was observed especially at Lake Winnebago where high commercial fishing did not change the catch per unit

effort for drum (Priegel 1971). Such resilience may have been a result of high fecundity for drum. Emphasis has been raised in the literature on the variable mortality of drum larvae and the influence upon year-class strength. To what extent larval mortality could influence year-class strength and potential compensation following catastrophic mortality has not yet been made clear. However, due to the high fecundity of drum, even slight changes in that mortality rate could have a major influence on recruitment and thus compensatory potential. The cases examined suggest that early survival of drum improved after catastrophic events decreased competition. However, the evidence is not conclusive. No other compensatory mechanisms have been documented for drum.

SYNTHESIS

LIFE HISTORY STRATEGIES AS PREDICTORS OF COMPENSATION

The three clupeids studied, alewife, threadfin shad, and gizzard shad, perform fairly similar functions in an ecosystem - all are pelagic planktivores and forage fishes. Thus we expected similarities in compensatory strategies for these species as much as for any group of species on which we concentrated. Indeed there were similarities, but compensatory response was not exactly the same for each. All three were resilient species. Density-dependent growth has been demonstrated for all three, and density-dependent early survival is strongly suspected as an important factor in compensation after a catastrophe. Competition or predation is probably the operating mechanism mediating early survival and thus controlling populations of these clupeids. Fecundity, age at maturity, multiple spawnings per year, and, rarely, cannibalism occasionally contribute to population regulation, but cannot bring about explosive increases in these species as the competition-predation-growth-survival interaction can. After a catastrophic event, low densities and decreased competition permit increased growth, especially of young, which in turn lessens predation mortality and perhaps stress mortality. The notable difference between these three species relates to the larger ultimate size and faster growth of gizzard shad. Predators can control gizzard shad even less easily than alewife or threadfin shad because of their size, thus predation is a weaker compensatory mechanism for gizzard shad. However, gizzard shad do not increase their fecundity with age and size as alewife and threadfin do, so gizzard shad are lacking a mechanism for increase that the other two species have. Gizzard shad may be similar to freshwater drum in their means of compensating, predation being a weaker regulator for a fast-growing species after a certain size is reached. It should be noted that many of the clupeid case histories show compensatory predation, but usually in systems where predators have been stocked.

Further evidence for the importance of first-year survival is found in marine research. Although recruitment generally cannot be predicted from abundance of early, planktonic larvae (E.B. Cohen et al. unpub. ms., Natl. Marine Fish. Serv., Northeast Fish. Ctr., Woods Hole Laboratory, Woods Hole, MA; Saville and Schnack 1981), there is a better relationship between juvenile, age-0 or age-1 fish and adults. Year-class strength is believed to be determined during the early planktonic stage, but the timing of the critical stage is still unknown (Saville and Schnack 1981). Cohen et al. (unpub.) showed that haddock (*Melanogrammus aeglefinus*) post-larval mortality is at least as great as larval fish mortality, and that predation on pre-recruits extends up to 100% of estimated pre-recruit production. Thus for haddock, mortality between the planktonic stage and late in the first year determines year-class strength.

Cushing (1974) discussed density-dependent regulation of larval fish mortality and adult mortality in fish. Abundance is controlled during the larval fish drift period through the mechanism of density-dependent growth and mortality. Gulland (1965) distinguished a fine and coarse control on

populations. The coarse control occurred at the larval fish stage. Numbers were adjusted through mortality in the drifting period with those reaching favorable habitat and food conditions surviving this high mortality stage. The fine control occurred later, and adjusted population levels depending on predation, food supply, and habitat constraints. Throughout their lives, Gulland stressed, fish are food and predators; predation is a major form of death in the sea. Fish pass through predation fields as they grow older, so the less dense they are the less chance they have of being eaten and the greater chance they have of getting adequate food. Larvae exploit their food supply to the maximum using density-dependent mechanisms with the fine tuning coming later.

Species can be grouped into several categories based on their life history patterns. Behavior traits and biological characteristics, particularly trophic level, narrow their potential compensatory mechanisms and serve to stratify species groups in general terms. For example, bluegill are prolific spawners which are not known to be strongly cannibalistic. Yearlings and adults eat similar food, and predation is usually a weak force on these fish because of the presence of vegetation into which they can escape. This leads to poor self-regulation and extensive stunting which is amply documented in the literature. Another example of habitat affecting control by predation is seen for the channel catfish (*Ictalurus punctatus*), which shows better survival in turbid water than clear water (Marzolf 1957; Davis 1959). Species whose food is similar between older juveniles and adults, and where both stages inhabit the same waters such as bluegill and threadfin shad, have more potential for intraspecific competition than species for which food or habitat significantly differs between juvenile and adult. Thus density-dependent growth is likely to be more marked for these species. Species like the clupeids produce hundreds of thousands of eggs apiece. They are preyed on heavily by predators but seldom kept at a constant level of abundance. Usually density-dependent mechanisms, such as disease or winterkill, because of poor condition due to inadequate food, act as ultimate controls on population numbers. Yellow perch on the other hand are cannibalistic and as well usually favorite prey of cohabiting predators. Thus, yellow perch populations tend toward a greater degree of self-regulation, and thus stability, than the former two species. A final category of fish is the top predator. Fish like northern pike and walleye are entirely carnivorous, including cannibalistic; thus they tend to control their populations in early life stages. A dominant year class will depress cohabiting cohorts as it passes through the population. Populations are stable and stunting occurs less often than for centrarchids.

Another possible predictor of compensatory response is the natural range or rate of a given parameter. For example, a species with high fecundity may have more range of variability than a species with low fecundity, thus more possibility of a compensatory change in fecundity. Also, a highly fecund species with a low survival rate has more room to increase early survival than a species with low fecundity and high survival. Fast-growing fish usually have a wider range of growth than slow-growing ones, thus may be more plastic in their response.

RESILIENT AND STABLE SPECIES

Holling (1973) described resilience as "the persistence of systems and of their ability to absorb change ... and still maintain the same relationships..." Stability, on the other hand, is the ability to return to an equilibrium. In the sense of these definitions, we classified each species (Fig. 2); e.g., alewife, threadfin shad, gizzard shad, freshwater drum, and rainbow smelt are resilient but not stable. Lake whitefish, walleye, yellow perch, and Pacific salmon are stable but not resilient. A trend in compensatory response can be seen among these groupings. Those stable species which are the most stable display the strong population-regulating mechanism of cannibalism; this is most marked for walleye and yellow perch. Resilient species tend to be prey rather than predators, so one of their important regulators is predation. Both resilient and stable species display density-dependent growth. With low densities, growth increases and faster-growing fish are less vulnerable to predation, including cannibalism. Resilient species generally have a greater intrinsic capacity for increase than stable species, so intraspecific competition is more apt to occur. Within each group, gradients in compensatory response are apparent. Freshwater drum and rainbow smelt, being piscivorous, have the potential to cannibalize their young so are somewhat more stable (better regulators) than the clupeids. Lake whitefish are primarily benthic feeders, and adult salmon are spatially separated from their young, so cannibalism is not as important as it is for large percids. As these concepts relate to compensation after a catastrophe, the absence of competition increases growth, and absence of cannibalistic or predatory adult fish permits increased survival, for all species. However, absolute fecundity prevents some species (salmon, lake whitefish) from increasing as fast as species like freshwater drum or gizzard shad. Some resilient species such as alewife or threadfin shad display a suite of responses - fecundity, age at maturity, condition, growth - that, in addition to increased early survival, allow them to persist through repeated stresses and mass mortalities. This classification scheme may be an oversimplification, but we include it here for the purpose of provoking further thought.

COMMUNITY EFFECTS

Catastrophic events sometimes result in shifts in species composition. We found several examples of this. Introductions, compensatory predation, extreme overfishing, and perhaps competitive interference have resulted in species abundance changes in the Great Lakes. Introduction of the alewife and overfishing adversely affected lake herring and other chubs until stocks collapsed (Smith 1970). Yellow perch were also depressed by alewife. Changes in the Great Lakes are considered by Holling (1973) to represent changes to different domains of attraction, where stability is now maintained at a different abundance level and species composition than previously. Genetic introgression of chubs may prevent their recovery to previous abundance levels or modes of life.

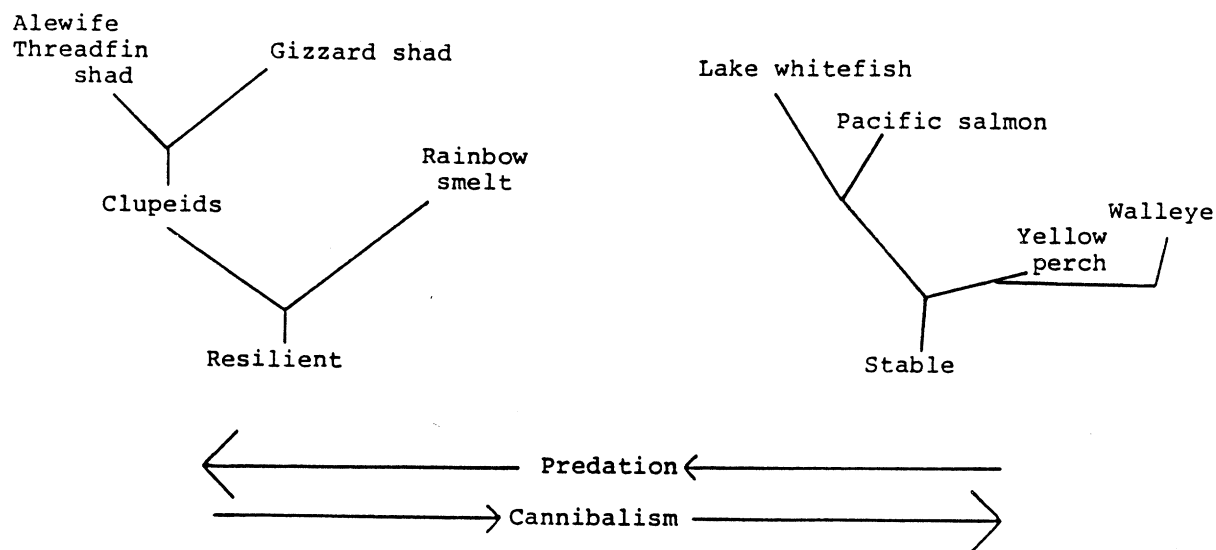


FIG. 2. Resilience versus stability, as defined by Holling (1973), of the species investigated for this report. Species on branches close to one another are relatively similar in their resilience or stability.

There are several examples of community shifts between populations of yellow perch and other species. Eshenroder (1977) traced part of the yellow perch decline and subsequent dominance changes in Saginaw Bay to the invasion of the exotic alewife, a phenomenon also noted by Wells (1977). The mechanism for this decline in Lake Michigan was hypothesized to be predation on larval yellow perch by alewife. Another example is given by Burrough et al. (1979) for the Eurasian perch in England. Here interactions between rudd, a cyprinid, and the roach, caused perch populations to decline when roach populations assumed dominance. They suggested competition for food at younger stages as the mechanism. Svardson (1976) studied a lake with roach and yellow perch present. With increased acidification, roach populations declined and yellow perch, which are less sensitive to acid stress, immediately had increased growth, again suggesting competition for food as the depressing mechanism. Bardach (1951), in studies of Lake Mendota, saw increased growth of yellow perch concomitant with a decline in lake herring populations. Yellow perch have also disrupted communities. Fraser (1978) cites the case of salmonids being stocked in a Ontario oligotrophic lake and subsequent entry of yellow perch. He found that growth of the salmonids declined while perch growth improved. Lastly, there is a case where habitat alteration (infestation of Eurasian milfoil) caused a dramatic increase of yellow perch in a North Carolina lake at the expense of several other species (Borawa et al. 1978).

Selective removal of certain species may change community composition, but not necessarily in the way desired. Examples of this are the increase in gizzard shad when gizzard and threadfin shad were removed (Phillippy 1964), the increase in common carp when gizzard shad were removed (Rose 1957), and increased growth of thinned species (rough fish and panfish) rather than sport fish (Grice 1957).

ADVERSE EFFECTS OF COMPENSATION

While traditional fishery management theory holds that thinning a population to increase size of fish is desirable, there are disadvantages pertaining to a population which is compensating. An overview of many species shows a positive relationship between growth rate and mortality, and a negative relationship between those parameters and age at maturity. The energy costs of reproduction decrease energy available for growth and probably weaken the fish, increasing mortality (Roff 1984). Thus a population which is compensating for a catastrophic mortality by increasing spawning effort (increasing fecundity or decreasing age at maturity) may be increasingly vulnerable to other mortality factors such as disease or predation. An example of increased growth rates combined with early death is the gizzard shad in Lake Erie and Florida (Table 9). Since age at maturity has not been demonstrated to be size-specific for gizzard shad, we do not know yet whether growth and mortality are directly related, or indirectly through reproduction.

Evidence is also presented by Alm (1952) who found that strong year classes of Eurasian perch appear rarely, but they dominate for 10-15 years for both sexes in dystrophic lakes in Sweden. Growth is poor and individuals small, but longevity was extended. These are uncomplicated ecosystems, with only a few northern pike present. In eutrophic lakes, strong year classes occur more often and they do not dominate for a long period. Growth is good and perch attain large sizes. Schneberger (1935) and Harkness (1922) (cited in Alm 1952) pointed out that yellow perch which grew slowly attained a greater age. Alm (1952) concluded that natural mortality was the same in stunted and well balanced perch populations; however, in the latter lakes, intensive fishing, predation and intra- and interspecific competition increased mortality in the perch population.

Age of a spawning fish affects the quality of its eggs. Eggs from the youngest and oldest fish tend to have less yolk (Ricker 1977). There was a direct relationship between parental age of Eurasian smelts and whitefishes (female and male) and survival of larvae to the tail-bud stage, with some decreased egg survival from the very oldest parents (Korovina 1961 cited in Ricker 1977). Early maturing freshwater drum females had smaller eggs (Daiber 1953). Atlantic herring showed some tendency for egg weight to increase with age of the female. Some stocks showed a 2-10% increase in mean egg weight from one age-group to the next (Hempel and Blaxter 1967), and some mean egg weights increased 20-30% between recruits and older fish (Blaxter and Hempel 1963). The stocks which showed a statistically significant relationship between egg weight and length of female were the faster-growing stocks of smaller fish, while egg size and size of female were not correlated for stocks

of older, slower-growing fish (Hempel and Blaxter 1967). Bigger eggs produced longer larvae with heavier yolks and better survival when starved (Blaxter and Hempel 1963). Thus a fish population which is compensating by lowering age at maturity may be sacrificing egg quality and survival of larval fish, even though total number of eggs produced in a lifetime increases. Not only may lower age at maturity sacrifice egg quality, but also young fish may not exhibit appropriate spawning behavior or optimal seasonal timing (due to physiological constraints or behavior), resulting in failure of fertilization or poor survival. Thus increased spawning effort early in life may be wasted. Classical ecological theory indicates that the replacement of stocks with low reproductive capacity by stocks of high reproductive capacity may indicate environmental disturbance (Smith 1978), thus an increase in spawning effort by a population may be a result, and a sign, of increased mortality.

Fish populations may be capable of rebounding after a mass mortality, but mortality which removes part of the population may also remove a portion of its genetic variability. One of the least tractable and potentially most damaging effects of overfishing is changes in genetic stocks (Spangler et al. 1977). Thus the health and flexibility of the population and its ability to adapt to new stresses may be impaired. This is a hidden cost to compensation which cannot easily be measured. Loss of adaptability may mean that a population which recovers from a mass mortality one time cannot recover from another of a similar magnitude, particularly if the cause is different. Survivors of a cold kill may not be the same fish best adapted to survive a toxic spill.

A population which is compensating is probably not operating at optimal levels of growth and reproduction. Such a population is less resilient because its compensatory reserve has been reduced. It may be more vulnerable to environmental change or random factors and so be more likely to collapse entirely (Ricker 1954, 1977; Goodyear 1980). Extreme values of parameters related to compensatory mechanisms should be perceived as danger signals for the population's continued existence.

EFFECT OF CATASTROPHE TYPE

The type of catastrophic event may affect subsequent compensation of fish. Catastrophes affecting habitat may prevent compensation altogether. Examples of this include toxic spills and acid precipitation, where the substance that kills fish lingers in the system. If early survival is usually density-dependent, and a density-independent effect of a toxic substance is to decrease early survival, the population would be unable to compensate by that mechanism. We did not find good data for this specific a premise. There were, however, cases such as lake acidification where all fish were killed, and continuing acidification would prevent any recolonization and attempts to study compensation.

There have been other ramifications of habitat alteration such as an infestation of Eurasian milfoil, which afterwards favored yellow perch survival and populations increased (Borawa et al. 1978). Increased

acidification of lakes has led to a series of events for yellow perch. First competing species are eliminated, releasing competitive pressure and allowing perch population increases (Svardson 1976 cited in Burrough et al. 1979). As acidification increases further, adult reproductive failure occurs as adults apparently have more difficulty with calcium metabolism (Ryan and Harvey 1980; Beamish 1976). Thus, populations of younger fish (age 1-3) had reduced densities, less cannibalism from stressed and dying age-4-9 fish, and therefore grew better.

Certain events may affect some age-groups of fish more than others as was observed for yellow perch subjected to increased acidification. Stock collapse due to overfishing generally removes older fish first, and recruitment often then responds positively. Drawdown may directly kill young fish in the littoral zone, or may concentrate fish so that forage fish are subject to increased predation. The fishes we studied each had more than one compensatory mechanism available, thus were able to respond even if an option was removed. For example, forage fishes whose populations were reduced to a few adults produced large year classes, presumably through increased growth and survival of young, when age at maturity or fecundity compensation did not have time to occur. Elimination of one year class during its first year usually first served to increase growth of age-1 fish, then caused high recruitment the next year.

EFFECT OF GEOGRAPHIC AREA

Fishes from the fringes of their range could compensate in different ways than fishes in their normal range. Life history parameters may vary with latitude; for example, growth and reproductive effort of the lake herring decrease with more northerly latitude, probably due to the shorter growing season (Morin et al. 1982). Kelso and Bagenal (1977) examined yellow perch in unperturbed systems, which were rarely found and studied. They concluded perch inhabited harsh environments in these systems and that growth and recruitment were low and variable. Unperturbed systems usually had a wide range of age-groups present and a dominant year class was expressed for a longer period of time than in more perturbed systems. This natural variation in life history parameters implies that some compensatory mechanisms would operate more readily in certain parts of a fish's range. However, data gaps present a difficulty in answering this question. For no species is the documentation of compensatory response complete. If species X increases its fecundity in the south and increases its survival in the north, we usually do not know if it also increases fecundity in the north and survival in the south. Differences in a life history parameter between the fringes and center of a range may be attributable to the rest of the community, genetic stocks, or random factors.

One frequently seen effect of geographic area is the exacerbation of catastrophes. Populations in a harsh environment, such as gizzard shad in Lake Erie, may not be very healthy, so more are affected by a new mortality factor. Related to this are failed introductions, such as threadfin shad in Kansas and parts of Virginia and Ohio. These species, introduced beyond their

native range or expanding their range naturally, are vulnerable to cold kill; the farther north, the more likely that none will survive. Thermal plumes in North Carolina and Missouri allow threadfin shad to persist in lakes beyond their native range, where normally all would die of cold.

In a different vein, system scale has an effect on compensation. Large systems containing numerous stocks, including oceans, rivers, and the Great Lakes, are unlikely to undergo a catastrophe affecting all stocks of a given species. A localized event opens the way for immigration from adjoining stocks or populations. Immigration may prevent detection of compensation, or may actually prevent survivors of the catastrophe from compensating because fish densities do not remain low for long. We found many examples of this, particularly in rivers, where fish kills are easily observed. Catastrophic overfishing is sometimes an exception, because fishermen may range widely and affect all stocks of a species, depleting the species so that immigration becomes insignificantly small. Man, as a predator, can act in a depensatory manner because prey have had no time to evolve compensatory mechanisms strong enough to maintain their populations (Radovich 1979).

RESEARCH RECOMMENDATIONS

INTRODUCTION

In this section we recommend future research which, we believe, will significantly improve understanding of compensatory mechanisms. Our criteria for choosing research recommendations were: (1) to fill in the most important data gaps, improving our general knowledge of compensation, (2) efficiency, i.e., obtaining maximum information for minimum effort or expense, and (3) feasibility of successfully obtaining results, or amenability of the parameter to research and measurement. We have proposed further research on several species, such as clupeids and yellow perch, for which compensation is already partially understood, with the purpose of completing our knowledge and possibly generalizing to similar species. Study of mechanisms affecting, and rates of, early survival are emphasized for several species because, although many researchers believe compensation frequently occurs in early life, early survival is not well studied empirically. Recent techniques of aging fish larvae now allow us to calculate mortality, pinpoint "critical periods," and perhaps correlate times of mortality with environmental factors or community interactions to discover the important mechanisms, compensatory or not, controlling early survival. We have also attempted to derive methods of obtaining useful results from accidental catastrophes, and of obtaining maximum information from existing monitoring programs. See RELATIVE IMPORTANCE OF RECOMMENDED RESEARCH for a ranking of these programs.

In future studies of compensation, researchers should address the unit or level at which compensation operates. We have assumed through most of this report that previous studies concerned one integrated population, an aggregation of stocks, which was affected as a unit by a catastrophic mortality and subsequent compensation. However, many of these studies may have actually represented some other scenario such as extinction of one stock and its replacement by another, perhaps with slightly different values of life history parameters. In such cases compensatory mechanisms would not be operating in the same fashion as they appear to. The most relevant results would be obtained from a system where the species under investigation was of one integrated population, and this is more likely to occur in a pond or small lake than in a larger system.

Power plant cooling ponds and public water supply reservoirs offer opportunities for experimental manipulation of populations. System scale for such research trades off controllability - too large a system and the variables and logistics become immense - versus reality: too small a system may have too few species or too little physical variety to resemble an actual ecosystem. Also, large systems are complicated by the above-mentioned stock versus population problem. Many cooling ponds and reservoirs are appropriate sizes for population experiments, with natural species complexes sometimes available. Exploitation usually can be controlled completely by the utility. Such ponds and reservoirs exist in many geographic regions, permitting a variety of species and communities to be studied.

CLUPEIDS

The most notable data gap for alewife, threadfin shad, and gizzard shad is survival of age-0 fish at various densities. Increased survival of young, thought to be an important result of compensation for these species, could and should be quantified and its variations delimited. We suggest a site such as Lake Norman, North Carolina, where threadfin shad are subject to repeated winter kills and respond by building up large populations each year. This site would be compared with a more southerly lake, perhaps in Florida, where mass mortalities are rare. Length-frequencies for larvae and juveniles at each site could be adjusted using otoliths to reflect actual age of the fish, and densities at each age used to calculate survival. Nutritional condition of the larvae should be compared between sites (methods in Theilacker 1978) for evidence of competition or adequacy of food supply, and adult fishes' stomachs checked in an attempt to quantify predation. If as we suspect, survival of larval and juvenile fish is greater where mass mortalities are common, it would demonstrate the existence of compensatory mechanisms, and the difference between sites should help quantify compensatory reserve.

A widely fluctuating forage population undergoing compensatory predation is available for study: the Lake Michigan alewife. Population abundance indices, growth, larval fish densities, and other data are available at the Great Lakes Fishery Laboratory of U.S. Fish and Wildlife Service, back into the 1960s, and from our Cook Nuclear Plant and Campbell Plant studies at the Great Lakes Research Division for 1973-1982 and 1977-1981 respectively. The decline of the alewife in the last few years offers a unique opportunity for further study. Ongoing food habits studies for salmon (Michigan and Wisconsin Sea Grant) should be correlated with population abundance to see if compensatory predation is continuing. Also we recommend collection of growth and survival data to compare with earlier years when alewife was abundant in Lake Michigan. A relatively small amount of additional field collection would be needed, as various agencies mentioned above have already done a great deal of the work. We believe this is one of the better, most easily accomplished opportunities to quantify some parameters for a large system.

Interesting results could be obtained if stocking practices in Lake Michigan were changed. A large-scale manipulation might be performed by stocking many more predators (e.g., lake trout or salmon) than usual and measuring whether survival, growth, or any other factor changes for alewife. Compensatory response may already be stretched for alewife; increasing stocking may finally drive alewife populations to low levels or zero. Increase of stocking might thus test compensatory capacity of alewife. Naturally, state Departments of Natural Resources and U.S. Fish and Wildlife Service would have to be convinced to allow this. One point in favor in their view might be improvement in fishing for the sport angler.

PACIFIC SALMON

Compensatory mechanisms are well understood for Pacific salmon in comparison with most other species. Egg mortality is known to have density-dependent aspects and to be fairly important in population regulation. One aspect of the compensatory reserve of Pacific salmon could be tested by experiments to determine egg mortality at different densities. Such experiments have been done for pink and chum salmon (Hunter 1959), and should be done in more detail and for other species as well. We envision laboratory experiments or in-stream enclosure experiments with different egg densities and different substrates to measure mortality and test the rate of dislodging due to spawning in marginal habitat or digging up and reburying of eggs. Sources of mortality - oxygen depletion, fungus infection, waste product buildup, dewatering, predation - and their relative importance should be discovered.

YELLOW PERCH

In order for a research effort to be useful to EPRI, it should be generic in nature, with results generally applicable. Growth is one of the final integrators of a vast plethora of interacting factors. It should be conceptually possible to develop a set of growth equations or a model for a number of regions across the U.S. Yellow perch may be a particularly good possibility for this effort, since large and extensive data sets on growth and other vital functions are available in the literature. These data would be used to generate maxima standards for various regions, which would give a upper limit for yellow perch growth. A utility could then determine current growth conditions in the population impacted or of interest and compare these with the growth maxima for that region to quantitatively derive an estimate of compensatory capacity.

More restricted studies could be done both to test the model and to provide parameters for it. Some method for handling predation and cannibalism may have to be introduced into the equations. Pond experiments could be conceived with a factorial design using as factors: predation, harvest levels (0, 25, 50, 75%), age-group harvested (larvae, YOY, adults), competition (with bluegills, cyprinids), and possibly nutrients. Data from these experiments could shed considerable light on compensatory capacity and interactions of an impacted perch community as well as generate data on growth and response of various age-groups to catastrophic loss.

FRESHWATER DRUM

Research on freshwater drum and its compensatory potential should focus upon the factors affecting larval fish mortality and the subsequent relationships to year-class strength. High fecundity normally found for drum would suggest a small change in the larval fish mortality rate could have a large effect on recruitment. Therefore, a catastrophic event impacting drum and the subsequent recovery of the population would depend largely on any

change in the survival of the eggs and larvae. To first determine whether any change in larval drum mortality influences recruitment and year-class strength, a means to eliminate large numbers of larvae is needed. By varying the magnitude of this loss of larvae, one could then observe the relative impact upon the recruitment and year-class strength in later years. Such an experiment might be done with a population at a reservoir such as described by Walburg (1971). Here flushing of larvae over a dam accounted for substantial losses of drum larvae from the reservoir. Such losses could be then controlled by adjusting the passage of water through the dam or at least measured in the discharge. The subsequent impact on drum of variable losses of larvae could be followed in year-class strength. One problem with using reservoirs would be the potential immigration of larvae from upriver which could be significant. Such immigrants would have to be taken into account in assessing losses of larvae to the reservoir drum population.

Determining the mechanisms of larval fish mortality for freshwater drum in natural populations and whether they were density-dependent would be complicated if several of these mechanisms (i.e., disease or parasitism, predation, starvation, stress mortality) operated simultaneously. One approach would be to monitor all the potential causes of mortality, including potential density-independent ones such as temperature, and correlate their variation to changes in larval mortality rate. This approach would probably be the most relevant in describing the relative effects of several factors. However, this method would require good measures for disease, parasitism, predator consumption of drum larvae, larval fish feeding in relation to food supply, and indications of stress. Such measures are not necessarily easily made. Furthermore, larval fish mortality would also need to be monitored for several years to account for variation in density-dependent and density-independent parameters. Larval fish mortality rates would be quantified by sampling with plankton nets to give a length-frequency relationship (see Cada and Hergenrader 1980) along with larval otolith samples to determine their age. Since subtle changes in mortality rates could have a major effect on recruitment, high precision in sample estimates of larval abundance as well as potential causes of mortality would be needed. Large lakes tend to be more variable environments with greater mobility of fish and thus more difficult to obtain high precision in sampling. Therefore, we suggest a small lake or pond with a known drum population could be best used to conduct the analysis suggested here. Such a situation might also offer the advantage of controlling to some degree some of the potential causes of larval fish mortality, such as predation, and thus give a better idea of the impacts of various population regulating factors.

FOLLOW-UP STUDIES

We found many examples in the literature of mass fish mortalities where no follow-up data were collected; these were more numerous than studies with subsequent data. We recommend an opportunistic approach. A fund could be established to take advantage of unfortunate accidents resulting in fish kills. When a mortality occurs, a small-scale study could begin, perhaps performed by university professors and students to limit costs. Fish could be

sampled at fairly wide intervals immediately after the mortality and when the population had recovered, a year or two later. Easily collected data would include length, weight, age, fecundity, sex ratio, and age at maturity. These parameters could be compared between the immediate post-mortality and later times. While detailed quantitative studies would not be carried out this way, the result would still be more useful than much previous work which only presents amounts of dead fish. Examples of studies that should have been continued, and perhaps still should be, are: Alcorn et al. (1980), Kushlan (1974), Turnpenny and Williams (1981), Crunkilton et al. (1980), Bury (1972), Johnston and Cheverie (1980), and Olmsted and Cloutman (1974); all are included in the annotated bibliography, Appendix 1. Various agencies are conducting bioassay and toxicity research, and accidental introduction of toxic materials into our waters occurs often enough to provide much information without the need for EPRI to put high priority on an experimental approach to compensation after toxic spills.

To implement such a program, EPRI would first need to contact state agencies to which toxic spills must be reported, and ask to be notified when such spills occur. Industry biologists and various newsletters or bulletins may lead to knowledge of winterkills, disease epidemics, or other catastrophic mortalities. We recommend that EPRI set up a small committee of several people, both from the utility industry and outside it, who would (1) set up, in advance, a contact list of people who could conduct the sampling, (2) authorize the sampling, and (3) set up guidelines for sampling methods, design, and analysis, including quality control and data set comparability. The committee or another consultant may be required to integrate results of many such small studies into the larger picture of compensatory response.

EXPANSION OF ONGOING MONITORING PROGRAMS

Because of regulatory and monitoring requirements, the power industry has a number of data sets which could be used to demonstrate compensation given the manpower to analyze the data. Many of these data sets are of limited scope and have the same problems, but they could still be used to determine some life history parameters, particularly if some improvements or additions are made to sampling and analysis. Population abundance or densities of adult and larval fish and numbers of fish impinged or entrained over time are tools for helping demonstrate the compensatory reserve of fish populations. Frequently during monitoring studies, biologists collect other data such as sizes of fish, from which growth rates, age structure, or survival could be determined with a relatively small amount of extra effort. Other examples of neglected parameters are fecundity, age at maturity, predation/cannibalism, and sex ratio. We recommend that EPRI contribute funding to improve industry monitoring studies. Measurement of a few more parameters from fish that already must be collected would help fill out the picture of compensatory responses in these populations.

On a smaller scale, we recommend that EPRI at least assign or fund a few people to interpret already-existing data sets. Many industry biologists are aware of or have contributed to extensive population estimates and

descriptions of fish distributions, but have had no time to summarize or interpret the masses of data available. There are several examples from people we spoke to for this project (Table 12). Age and growth, survival, age at maturity, and fecundity data, combined with their existing work on biomass, numbers, and distribution of fish, would be very useful in quantifying compensatory reserve.

RELATIVE IMPORTANCE OF RECOMMENDED RESEARCH

We have ranked research programs we recommended according to three criteria: (1) value of the information to our understanding of compensatory response to a catastrophe, (2) relatively large amount of information obtained for a relatively small effort, and (3) feasibility of successfully obtaining results. The resultant ranking is:

1. Comparison of threadfin shad between Lake Norman and more southern lake
2. Yellow perch pond experiments
3. Compensatory predation on Lake Michigan alewife
4. Follow-up studies
5. Expansion of monitoring programs
6. Yellow perch growth models
7. Freshwater drum early life history
8. Pacific salmon egg experiments
9. Large-scale predator stocking in Lake Michigan

TABLE 12. Unpublished or unanalyzed data sets.

Species	Data or life history parameters	Organization having data
Alewife	Age and growth Relative abundance	Wisconsin Electric Power Co.
Alewife	Age and growth Mortality estimates Biomass	U.S. Fish and Wildlife Service
Threadfin shad	Abundance: decimation of population and rebound Age and growth Plankton (food) Impingement	Duke Power Company
Bloater	Age and growth CPUE	Wisconsin Dept. of Natural Resources
Rainbow smelt	Age and growth Relative abundance	Wisconsin Electric Power Co.
Rainbow smelt	Length-frequency, CPUE	Wisconsin Dept. of Natural Resources
Common carp	Renovation/removal (Tons removed)	Wisconsin Dept. of Natural Resources
Yellow perch	Summer kill	Duke Power Company
Bay anchovy (<i>Anchoa mitchilli</i>)	Maturity, competition, age composition, sex ratio, abundance, mortality, fecundity, spawning frequency	Public Service Electric and Gas Co.
Bay anchovy	Abundance Impingement	Baltimore Gas and Electric Co.
Bay anchovy	Abundance	Lawler, Matusky and Skelly Engineers
Bay anchovy	Winterkill	New Jersey Central Power and Light Co.

REFERENCES

- Adams, S.M., R.B. McLean, and M.M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Can. J. Fish. Aquat. Sci. 39:1175-1184.
- Agersborg, H.P.K. 1930. The influence of temperature on fish. Ecology 11:136-144.
- Alcorn, D.J., L.E. Fancher, and J.G. Moss. 1980. Harbor seal and fish populations before and after a sewage spill in south San Francisco Bay. Calif. Fish and Game 66:238-239.
- Alm, G. 1946. Reasons for the occurrence of stunted fish-populations. Rep. Swedish State Inst. Freshwater Fish. Res. Drottningholm 25.
- Alm, G. 1952. Year class fluctuations and span of life in perch. Rep. Inst. Freshwater Res. Drottningholm 33:17-38.
- Anderson, E.D., and L.L. Smith, Jr. 1971. Factors affecting abundance of lake herring (*Coregonus artedii* Lesueur) in western Lake Superior. Trans. Amer. Fish. Soc. 100:691-707.
- Anthony, D.D., and C.R. Jorgensen. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960-1976. J. Fish. Res. Board Can. 34:1703-1709.
- Bagenal, T.B. 1970. An historical review of the fisheries investigations of the Freshwater Biological Association, mainly at the Windermere Laboratory. J. Fish. Biol. 2:83-101.
- Bagenal, T.B. 1977. Effects of fisheries on Eurasian perch (*Perca fluviatilis*) in Windermere. J. Fish. Res. Board Can. 34:1764-1768.
- Bagenal, T.B. 1982. Experimental manipulations of the fish populations in Windermere. Hydrobiologia 86:201-206.
- Bailey, M.M. 1969. Age, growth, maturity, and sex composition of the American smelt, *Osmerus mordax* (Mitchill), of western Lake Superior. Trans. Amer. Fish. Soc. 93:382-395.
- Bailey, W.M. 1978. A comparison of fish populations before and after extensive grass carp stocking. Trans. Amer. Fish. Soc. 107:181-206.
- Baldwin, N.S., R.W. Saalfeld, M.A. Ross, and H.J. Buettner. 1979. Commercial fish production in the Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 3:187 p.
- Bardach, J.E. 1951. Changes in the yellow perch population of Lake Mendota, Wisconsin, between 1916 and 1948. Ecol. 32:719-728.

- Beamish, R.J. 1976. Acidification of lakes in Canada by acid precipitation and the resulting effects on fishes. In Proc. Internat. Symp. Acid Precip. Forest Ecosystem. USDA Forest Ser. Gen. Tech. Rep. NE-23. 477 pp.
- Beckman, W.C. 1941. Increased growth rate of rock bass, *Ambloplites rupestris* (Rafinesque), following reduction in the density of the population. Trans. Amer. Fish. Soc. 70:143-148.
- Beckman, W.C. 1943. Further studies on the increased growth rate of the rock bass *Ambloplites rupestris* (Rafinesque), following the reduction in density of the population. Trans. Amer. Fish. Soc. 72:72-78.
- Beckman, W.C. 1950. Changes in growth rates of fishes following reduction in population densities by winterkill. Trans. Amer. Fish. Soc. 78:82-90.
- Beers, G.D., and W.J. McConnell. 1966. Some effects of threadfin shad introduction on black crappie diet and condition. J. Arizona Acad. Sci. 4:71-74.
- Beeton, A.M. 1961. Environmental changes in Lake Erie. Trans. Amer. Fish. Soc. 90:153-159.
- Bell, G., P. Handford, and C. Dietz. 1977. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*). J. Fish. Res. Board Can. 34:942-953.
- Bergstedt, R., and R. O'Gorman. 1983. Lake Ontario fish stocks: surveillance and status of fish populations. Progress in Fishery Research 1983. Great Lakes Fish. Lab., U.S. Fish and Wildl. Serv., Ann Arbor, MI:15-16.
- Berry, F.H., M.T. Huish, and H. Moody. 1956. Spawning mortality of the threadfin shad, *Dorosoma petenense* (Günther), in Florida. Copeia 1956:192.
- Berst, A.H., and G.R. Spangler. 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29:877-887.
- Beverton, R.J.H., and S.H. Holt. 1957. On the dynamics of exploited fish populations. Fishery Invest. Lond. Ser. 2(19).
- Bidgood, B.F. 1973. Divergent growth in two lake whitefish (*Coregonus clupeaformis*) populations. J. Fish. Res. Board Can. 30:1683-1696.
- Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. J. Animal Ecol. 17:15-26.
- Blaxter, J.H.S., and G. Hempel. 1963. The influence of egg size on herring larvae (*Clupea harengus*). J. Cons. Perm. Explor. Mer 28:211-240.

- Boaze, J.L., and R.T. Lackey. 1974. Age, growth, and utilization of landlocked alewives in Claytor Lake Virginia. *Prog. Fish-Cult.* 36:163-164.
- Bodola, A. 1966. Life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in western Lake Erie. *U.S. Fish and Wildl. Serv. Fish. Bull.* 65:391-425.
- Borawa, J.C., J.H. Kerby, M.T. Huish, and A.W. Mullis. 1978. Currituck Sound fish populations before and after infestation by Eurasian Water-Milfoil. *Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agencies* 32:520-528.
- Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28-35. Cited in C.C. Kohler (1980).
- Brown, E.H., Jr. 1968. Population characteristics and physical condition of alewives, *Alosa pseudoharengus*, in a massive dieoff in Lake Michigan, 1967. Great Lakes Fishery Commission, Technical Report No. 13, 20 pp.
- Brown, E.H., Jr. 1970. Extreme female predominance in the bloater (*Coregonus hoyi*) of Lake Michigan in the 1960's. pp. 501-514 in: C.C. Lindsey and C.S. Woods (eds.), *Biology of coregonid fishes*. Univ. Manitoba Press, Winnipeg, Manit.
- Brown, E.H., Jr. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949-70. *J. Fish. Res. Board Can.* 29:477-500.
- Bryant, H.E., and A. Houser. 1968. Growth of threadfin shad in Bull Shoals Reservoir. *Proc. Ann. Conf. S.E. Assoc. Game and Fish Comm.* 22:275-283.
- Burns, J.W. 1966. Threadfin shad. pp. 481-488 in: A. Calhoun (ed.) *Inland fisheries management*. California Dept. of Fish and Game, Sacramento.
- Burrough, R.J., and C.R. Kennedy. 1979. The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). *J. Fish Biol.* 15:93-109.
- Burrough, R.J., P.R. Bregazzi, and C.R. Kennedy. 1979. Interspecific dominance amongst three species of coarse fish in Slapton Ley, Devon. *J. Fish Biol.* 15:535-544.
- Bury, R.B. 1972. The effects of diesel fuel on a stream fauna. *Calif. Fish and Game* 58:291-295.
- Busch, W.-D.N., R.L. Scholl, and W.L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-1970. *J. Fish. Res. Board Can.* 32:1733-1743.

- Butler, R.L. 1965. Freshwater drum, *Aplodinotus grunniens*, in the navigational impoundments of the upper Mississippi River. Trans. Amer. Fish. Soc. 94:339-349.
- Butler, R.L., and L.L. Smith Jr. 1949. The age and rate of growth of the sheepshead, *Aplodinotus grunniens* Rafinesque, in the upper Mississippi River navigation pools. Trans. Amer. Fish. Soc. 79:43-54.
- Cada, G.F., and G.L. Hergenrader. 1980. Natural mortality rates of freshwater drum larvae in the Missouri River. Trans. Amer. Fish. Soc. 109:479-483.
- Carlander, K.D. 1945. Age, growth, sexual maturity, and population fluctuations of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Trans. Amer. Fish. Soc. 73:90-107.
- Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. Trans. Amer. Fish. Soc. 102:739-744.
- Chevalier, J.R. 1977. Changes in walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance, 1924-75. J. Fish. Res. Board Can. 34:1696-1702.
- Christie, W.J. 1968. Possible influences of fishing in the decline of Great Lakes fish stocks. Proc. Conf. Great Lakes Res. 11: 31-38.
- Christie, W.J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29:913-929.
- Christie, W.J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fishery Comm. Tech. Rep. No. 23. 65 pp.
- Christie, W.J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31:827-854.
- Christie, W.J., J.M. Fraser, and S.J. Nepszy. 1972. Effects of species introductions on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29:969-973.
- Clady, M.D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. J. Fish. Res. Board Can. 33:1887-1893.
- Clark, C. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. Cons. Int. Explor. Mer 36:7-14.
- Clepper, H. (ed.). 1979. Predator-prey systems in fisheries management. Sport Fisheries Institute.

- Colby, P.J. 1971. Alewife dieoffs: why do they occur? *Limnos* 4:18-27.
- Colby, P.J. 1973. Response of the alewives, *Alosa pseudoharengus*, to environmental change. pp. 163-198 in: W. Chavin (ed.). Responses of fish to environmental changes. C.C. Thomas, Springfield, IL.
- Colby, P.J., G.R. Spangler, D.A. Hurley, and A.M. McCombie. 1972. Effects of eutrophication on salmonid communities in oligotrophic lakes. *J. Fish. Res. Board Can.* 29:975-983.
- Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye *Stizostedion v. vitreum* (Mitchill 1818). FAO Fisheries Synopsis No. 119. 133 pp.
- Cole, C.F., J. Trenary, and S. Finkelstein. 1958. Experimental introduction of threadfin shad. *Ark. Game and Fish Comm., Ann. Rep.* Cited in Burns (1966).
- Combs, D.L. 1980. Fish population changes in Keystone Reservoir fourteen years after striped bass introductions. *Proc. Ann. Conf. S.E. Assoc. Fish. and Wildl. Agencies* 34:167-174.
- Cox, D.K., and C.C. Coutant. 1976. Acute cold-shock resistance of gizzard shad. pp. 159-161 in: G.W. Esch and R.W. McFarlane, eds. Thermal ecology II. Energy Research and Devt. Admin., Tech. Info. Ctr., U.S. Dept. Comm. Springfield, VA.
- Craig, J.F. 1980. Growth and production of the 1955 to 1972 cohorts of perch, *Perca fluviatilis* L., in Windermere. *J. Anim. Ecol.* 49:291-316.
- Craig, J.F., C. Kipling, E.D. LeCren, and J.C. McCormack. 1979. Estimates of the numbers, biomass and year-class strengths of perch *Perca fluviatilis* L. in Windermere from 1967 to 1977 and some comparisons with earlier years. *J. Anim. Ecol.* 48:315-325.
- Creaser, C.W. 1929. The food of yearling smelt from Michigan. *Papers Mich. Acad. Sci. Arts Letters* 10:427-431.
- Crecco, V., T. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. *Can. J. Fish. Aquat. Sci.* 40:1719-1728.
- Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? *Env. Biol. Fish.* 5:225-233.
- Crunkilton, R.L., J.M. Czarnecki, and L. Trial. 1980. Severe gas bubble disease in a warmwater fishery in the midwestern United States. *Trans. Amer. Fish. Soc.* 109:725-733.
- Cucin, D., and H.A. Regier. 1965. Dynamics and exploitation of lake whitefish in southern Georgian Bay. *J. Fish. Res. Board Can.* 23:221-274.

- Cushing, D.H. 1974. The possible density-dependence of larval mortality and adult mortality in fishes. pp. 103-111 in: J.H.S. Blaxter (ed.). The early life history of fish. Springer-Verlag, N.Y. 765 pp.
- Cushing, D.H. 1977. The problems of stock and recruitment. pp. 116-133 in: J.A. Gulland, ed. Fish population dynamics. Wiley & Sons, London.
- Daiber, F.C. 1953. Notes on the spawning population of the freshwater drum (*Aplodinotus grunniens* Rafinesque) in Western Lake Erie. Amer. Midl. Nat. 50:159-171.
- Davidoff, E.B., R.W. Rybicki, and K.H. Doan. 1973. Changes in the population of lake whitefish (*Coregonus clupeaformis*) in Lake Winnipeg from 1944 to 1969. J. Fish. Res. Board Can. 30:1667-1682.
- Davis, J. 1959. Management of channel catfish in Kansas. Univ. Kansas, Mus. Nat. Hist. Misc. Publ. No. 21. 56 pp.
- Dechtiar, A.O. 1972. New parasite records for Lake Erie fish. Great Lakes Fish. Comm. Tech. Rep. 17:20 p.
- Deelder, C.L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. Hydrobiologia 3:357-378.
- Eck, G.W., and L. Wells. 1983. Biology, population structure, and estimated forage requirements of lake trout in Lake Michigan. Technical Paper 111. U.S. Fish and Wildl. Serv.
- Elrod, J.H., R. O'Gorman, R. Bergstedt, and C.P. Schneider. 1980. Status of major forage fish stocks, U.S. waters of Lake Ontario. pp. 155-163 in: Great Lakes Fish. Comm., Lk. Ontario Committee Meeting, Appendix 13.
- El-Zarka, S. 1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay, Lake Huron. U.S. Fish Wildl. Serv. Fish. Bull. 59:365-415.
- Eschmeyer, R.W. 1936. Some characteristics of a population of stunted perch. Papers Mich. Acad. Sci., Arts and Letters 22:613-628.
- Eschmeyer, R.W., R.H. Stroud, and A.M. Jones. 1944. Studies of the fish population on the shoal area of a TVA mainstream reservoir. Rep. Reelfoot Lake Bio. Sta. 8:70-122.
- Eshenroder, R.L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34:1830-1838.
- Finucane, J.H. 1965. Threadfin shad in Tampa Bay, Florida. Quart. J. Florida Acad. Sci. 28:267-270. Cited in Johnson (1970).

- Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans. Amer. Fish. Soc. 114:328-337.
- Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. 162. Fish. Res. Board Canada/Ottawa. 422 p.
- Forney, J.L. 1965. Factors affecting growth and maturity in a walleye population. N.Y. Fish & Game J. 12:217-232.
- Forney, J.L. 1971. Development of dominant year classes in a yellow perch population. Trans. Amer. Fish. Soc. 100:739-749.
- Forney, J.L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Amer. Fish. Soc. 103:15-24.
- Forney, J.L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. J. Fish. Res. Board Can. 33:783-792.
- Forney, J.L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34:1812-1820.
- Forney, J.L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. N.Y. Fish Game J. 27:105-141.
- Forney, J.L. 1984. Status of fish stocks in Chautauqua Lake - 1983. Warmwater Fisheries Unit Job IV-b. 36 pp.
- Fraser, J.M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. Trans. Amer. Fish. Soc. 107: 505-517.
- Gaboury, M.N., and J.W. Patalas. 1984. Influence of water level drawdown on the fish populations of Cross Lake, Manitoba. Can. J. Fish. Aquat. Sci. 41:118-125.
- Gammon, J.R. 1971. The response of fish populations in the Wabash River to heated effluents. Proc. 3rd Nat. Symp. Radioecology:513-523.
- Gerking, S.D., ed. 1967. The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford. 495 pp.
- Gerking, S.D. 1976. Report on fecundity in the Waukegan-Zion sampling area of Lake Michigan for Commonwealth Edison. In: Nalco Envir. Sci., Compilation of reports relating to entrainment and impingement studies at Zion Generating Station, 1976, vol. II.

- Goodyear, C.P. 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations. pp. 186-195 in: W. Van Winkle, ed. Assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, New York.
- Goodyear, C.P. 1980. Compensation in fish populations. pp. 253-280 in Hocutt, C.H. and J.R. Stauffer, Jr. (eds.) Biological monitoring of fish. D.C. Heath & Co., Lexington, Massachusetts. 416 pp.
- Gordon, W.G. 1961. Food of the American smelt in Saginaw Bay, Lake Huron. Trans. Amer. Fish. Soc. 90:439-443.
- Graham, J.J. 1956. Observations on the alewife *Pomolobus pseudoharengus* (Wilson), in fresh water. Univ. Toronto Biol. Ser. 62, Publ. Ont. Fish. Res. Lab. 74. 43 pp.
- Great Lakes Fishery Laboratory. 1970. Physical and ecological effects of waste heat on Lake Michigan. U.S. Fish and Wildl. Serv. 101 pp.
- Grice, F. 1957. Effect of removal of panfish and trashfish by fyke nets upon fish populations of some Massachusetts ponds. Trans. Amer. Fish. Soc. 87:108-115.
- Grice, F. 1959. Elasticity of growth of yellow perch, chain pickerel, and largemouth bass in some reclaimed Massachusetts waters. Trans. Amer. Fish. Soc. 88:332-335.
- Gross, R.W. 1959. A study of the alewife *Alosa pseudoharengus* (Wilson) in some New Jersey lakes, with special reference to Lake Hopatcong. M.S. thesis, Rutgers Univ., New Brunswick, NJ.
- Gulland, J.A. 1965. Survival of the youngest stages of fish and its relation to year-class strength. Spec. Publs. int. Comm. N.W. Atlantic Fish. 6:365-371.
- Gulland, J.A., ed. 1977. Fish population dynamics. J. Wiley & Sons, London. 372 pp.
- Hale, J. 1960. Some aspects of the life history of the smelt (*Osmerus mordax*) in western Lake Superior. Minn. Fish Game Invest., Fish Invest. Rep. No. 204, p. 25-41.
- Hanson, D.L., and T.F. Waters. 1974. Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. Trans. Amer. Fish. Soc. 103:431-439.
- Harkness, W.J.K. 1922. The rate of growth of the yellow perch in Lake Erie. Univ. Toronto Stud. (Biol. Ser.) Publ. Ontario Fish. Res. Lab. 20:88-95.

- Hartman, W.L. 1972. Lake Erie: effects of exploitation, environmental changes, and new species on the fishery resources. J. Fish. Res. Board Can. 29:899-912.
- Havey, K.A. 1961. Restoration of anadromous alewives at Long Pond, Maine. Trans. Amer. Fish. Soc. 90:281-286.
- Healey, M.C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32:427-448.
- Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci. 37:255-267.
- Hempel, G., and J.H.S. Blaxter. 1967. Egg weight in Atlantic herring (*Clupea harengus* L.). J. Cons. Perm. int. Explor. Mer 31:170-195.
- Hesse, L.W., C.R. Wallace, and L. Lehman. 1976. Fishes of the channelized Missouri. Nebraska Game & Parks Comm. Tech. Ser. No. 4. 61 pp.
- Higley, D.L., and C.E. Bond. 1973. Ecology and production of juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, in a eutrophic reservoir. U.S. Natl. Mar. Fish. Serv. Bull. 71:877-891.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 20:1-228.
- Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4:1-23.
- Houser, A. 1960. Growth of freshwater drum in Oklahoma. Oklahoma Fish. Res. Lab. Rep. 78:13 p.
- Huish, M.T. 1957. Studies of gizzard shad reduction at Lake Beulah, Florida. Proc. Ann. Conf. S.E. Assoc. Game & Fish. Comm. 11:66-70.
- Hulsey, A.H. 1956. Effects of a fall and winter drawdown on a flood control lake. Proc. Ann. Conf. S.E. Assoc. Game & Fish. Comm. 10:285-289.
- Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16:835-886.
- Jackson, S.W., Jr. 1957. Comparison of the age and growth of four fishes from Lower and Upper Spavinaw Lakes, Oklahoma. Proc. Ann. Conf. S.E. Assoc. Game & Fish Comm. 11:232-249.
- Jenkins, R.M. 1957. The effect of gizzard shad on the fish population of a small Oklahoma lake. Trans. Amer. Fish. Soc. 85:58-74.

- Jensen, A.L. 1981. Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchill). J. Fish Biol. 19:557-574.
- Jester, D.B., and B.L. Jensen. 1972. Life history and ecology of the gizzard shad, *Dorosoma cepedianum* (LeSueur) with reference to Elephant Butte Lake. New Mexico State Univ. Agric. Exper. Sta. Res. Rep. 218. 56 pp.
- Jobes, F.W. 1952. Age, growth and production of yellow perch in Lake Erie. U.S. Fish Wildl. Serv. Fish. Bull. 52:205-266.
- Johnson, F.H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. 34:1633-1642.
- Johnson, J.E. 1970. Age, growth and population dynamics of threadfin shad, *Dorosoma petenense* (Günther), in central Arizona reservoirs. Trans. Amer. Fish. Soc. 99:739-753.
- Johnson, J.E. 1971. Maturity and fecundity of threadfin shad, *Dorosoma petenense* (Günther), in central Arizona reservoirs. Trans. Amer. Fish. Soc. 100:74-85.
- Johnson, L. 1976. Ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *Salvelinus alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33:2459-2488.
- Johnson, W.E. 1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Inst. Verein. Theor. Agnew. Limnol. 13:66-87.
- Johnston, C.E., and J.C. Cheverie. 1980. Repopulation of a coastal stream by brook trout and rainbow trout after endosulfan poisoning. Prog. Fish-Cult. 42:107-110.
- Jones, D.D., and C.J. Walters. 1976. Catastrophe theory and fisheries regulation. J. Fish. Res. Board Can. 33:2829-2833.
- Jude, D.J., and F.J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Can. J. Fish. Aquat. Sci. 42:1154-1157.
- Kelso, J.R.M., and T.B. Bagenal. 1977. Percids in unperturbed ecosystems. J. Fish. Res. Board Can. 34:1959-1963.
- Kendall, W.C. 1927. The smelts. Bull. U.S. Bur. Fish. 42:217-375.
- Kenyon, R.B. 1978. Growth changes in a population of whitefish in Lake Erie. N.Y. Fish Game J. 25:129-139.

- Kilambi, R.V., and R.E. Baglin, Jr. 1969. Fecundity of the threadfin shad, *Dorosoma petenense*, in Beaver and Bull Shoals Reservoirs. Trans. Amer. Fish. Soc. 98:320-322.
- Kimsey, J.B., R.H. Hagy, and G.W. McGammon. 1957. Progress report of the Mississippi threadfin shad, *Dorosoma petenensis atchafaylae* in the Colorado River for 1956. Calif. Fish & Game, Inland Fish Admin. Rep. 57-23. 48 pp. Cited in Johnson (1971).
- Kohler, C.C. 1980. Trophic ecology and impact of alewife in Claytor Lake, Virginia. Ph.D. dissertation. Virginia Polytechnic Inst. and State Univ., Blacksburg, VA. 192 pp.
- Kohler, C.C., and J.J. Ney. 1980. Piscivory in a land-locked alewife (*Alosa pseudoharengus*) population. Can. J. Fish. Aquat. Sci. 37: 1314-1317.
- Kohler, C.C., and J.J. Ney. 1981. Consequences of an alewife die-off to fish and zooplankton in a reservoir. Trans. Amer. Fish. Soc. 110: 360-369.
- Kushlan, J.A. 1974. Effects of a natural fish kill on the water quality, plankton, and fish population of a pond in the Big Cypress Swamp, Florida. Trans. Amer. Fish. Soc. 103:235-243.
- Laarman, P.W. 1969. Effects of a limited food supply on growth rates of coho salmon and steelhead trout. Trans. Amer. Fish. Soc. 98:393-397.
- Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford. 343 p.
- Lackey, R.T. 1970. Observations on newly introduced landlocked alewives in Maine. N.Y. Fish & Game J. 17:110-116.
- Lagler, K.F., and V.C. Applegate. 1942. Age and growth of the gizzard shad, *Dorosoma cepedianum* (LeSueur), with a discussion of its value as a buffer and as forage of game fishes. Invest. Ind. Lakes & Streams 2:99-110.
- Lambou, V.W. 1965. Observations on size distribution and spawning behavior of threadfin shad. Trans. Amer. Fish. Soc. 94:385-386.
- Larkin, P.A. 1977. Pacific salmon. pp. 156-181 in: J.A. Gulland (ed.). Fish population dynamics. John Wiley & Sons. New York. 372 pp.
- Lawler, G.H. 1965. Fluctuations in the success of year-classes of whitefish populations with special reference to Lake Erie. J. Fish. Res. Board Can. 22:1197-1227.
- Lawrie, A.H., and J.F. Rahrer. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29:765-776.

- Leach, J.H., and S.J. Nepszy. 1976. The fish community in Lake Erie. J. Fish. Res. Board Can. 33:622-638.
- Leach, J.H., M.G. Johnson, J.R.M. Kelso, J. Hartmann, W. Numann, and B. Entz. 1977. Responses of percid fishes and their habitats to eutrophication. J. Fish. Res. Board Can. 34:1964-1971.
- LeCren, E.D. 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27:287-334.
- LeCren, E.D. 1965. Some factors regulating the size of populations of freshwater fish. Mitt. Inst. Verein. Theor. Agnew. Limnol. 13:88-105.
- LeCren, E.D., C. Kipling, and J.C. McCormack. 1977. A study of the numbers of perch (*Perca fluviatilis* L.) in Windermere from 1941 to 1966. J. Anim. Ecol. 46:281-307.
- MacLean, J., and J.J. Magnuson. 1977. Species interactions in percid communities. J. Fish. Res. Board Can. 34:1941-1951.
- Mahon, R., and M. Ferguson. 1981. Invasion of a new reservoir by fishes: species composition, growth, and condition. Canadian Field-Naturalist 95:272-275.
- Mansfield, P.J., and D.J. Jude. In press. Alewife (*Alosa pseudoharengus*) survival during the first growth season in southeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 43.
- Marzolf, R.C. 1957. The reproduction of channel catfish in Missouri ponds. J. Wildl. Mgt. 21:22-28.
- McCammon, G.W., and C. von Geldern, Jr. 1979. Predator-prey systems in large reservoirs. pp. 431-442 in: H. Clepper, ed. Predator-prey systems in fisheries management. Sport Fishing Inst., Washington, D.C.
- McConnell, W.J., and J.H. Gerdes. 1964. Threadfin shad, *Dorosoma petenense*, as food of yearling centrarchids. Calif. Fish and Game 50:170-175.
- McFadden, J.T. 1977. An argument supporting the reality of compensation in fish populations and a plea to let them exercise it. pp. 153-183 in: W. Van Winkle, ed. Assessing the effect of power-plant induced mortality on fish populations. Pergamon Press, New York.
- McGee, M.V., J.S. Griffith, and R. McLean. 1977. Prey selection by sauger in Watts Bar Reservoir, Tennessee, as affected by cold-induced mortality of threadfin shad. Proc. Ann. Conf. S.E. Assoc. Fish & Wildl. Agencies 31:404-411.

- McLean, R.B., P.T. Singley, and D. Lodge. 1981. Threadfin shad impingement: population response. ORNL/NUREG/TM-339, Oak Ridge Natl. Lab., Oak Ridge, TN. 63 pp.
- Meekin, T.K., and R.L. Allen. 1974. Summer chinook and sockeye salmon mortality in the upper Columbia River and its relationship to nitrogen supersaturation. Wash. Dept. of Fisheries, Tech. Rep. 12: 127-153.
- Miller, R.B. 1947. The effects of different intensities of fishing on the whitefish populations of two Alberta lakes. J. Wildlife Mgt. 11:289-301.
- Miller, R.R. 1957. Origin and dispersal of the alewife *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. Trans. Amer. Fish. Soc. 86:97-111.
- Miller, R.R. 1960. Systematics and biology of the gizzard shad *Dorosoma cepedianum* and related fishes. U. S. Fish & Wildl. Serv. Fish. Bull. 173:370-392.
- Mills, E.L., and J.L. Forney. 1981. Energetics, food consumption and growth of young yellow perch in Oneida Lake, New York. Trans. Amer. Fish. Soc. 110:479-488.
- Minckley, W.S., and L. Krumholtz. 1960. Natural hybridization between the clupeid genera *Dorosoma* and *Signalosa* with a report on the distribution of *S. petenense* (Günther). Zoologica 45:171-182.
- Moody, H.L. 1957. A fisheries study of Lake Panasoffkee, Florida. Quart. J. Florida Acad. Sci. 20:21-88.
- Morin, R., J.J. Dodson, and G. Power. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), and round whitefish (*Prosopium cylindraceum*) populations of eastern James-Hudson Bay. Can. J. Fish. Aquat. Sci. 39:958-967.
- Nakashima, B.S., and W.C. Leggett. 1975. Yellow perch (*Perca flavescens*) biomass responses to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec-Vermont. J. Fish Res. Board Can. 32:1785-1797.
- Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9:450-491.
- Nelson, W.R. 1974. Age, growth, and maturity of thirteen species of fish from Lake Oahe during the early years of impoundment, 1963-68. U.S. Fish and Wildl. Tech. Pap. 77:29 pp.

- Nelson, W.R., and C.H. Walburg. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River reservoirs. J. Fish. Res. Board Can. 34:1748-1763.
- Nepszy, S.J. 1977. Changes in percid populations and species interactions in Lake Erie. J. Fish. Res. Board Can. 34:1861-1868.
- Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37:11-19.
- Nigro, A.A. 1980. Reproduction and early life history of a landlocked population of alewife (*Alosa pseudoharengus*) in Claytor Lake, Virginia. M. S. thesis, Virginia Polytechnic Inst. and State Univ., Blacksburg, VA. 85 pp.
- Norden, C.R. 1967. Age, growth, and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Trans. Amer. Fish. Soc. 96:387-393.
- Northcote, T.G. 1972. Kootenay Lake: man's effects on the salmonid community. J. Fish. Res. Board Can. 29:861-865.
- Odell, T.T. 1934. The life history and ecological relationships of the alewife (*Pomolobus pseudoharengus* [Wilson]) in Seneca Lake, New York. Trans. Amer. Fish. Soc. 64:118-126.
- O'Gorman, R. 1974. Predation by rainbow smelt (*Osmerus mordax*) on young-of-the-year alewives (*Alosa pseudoharengus*) in the Great Lakes. Prog. Fish-Cult. 36:223-224.
- Olmsted, L.L., and D.G. Cloutman. 1974. Repopulation after a fish kill in Mud Creek, Washington County, Arkansas following pesticide pollution. Trans. Amer. Fish. Soc. 103:79-87.
- Parsons, J.W. 1970. Walleye fishery of Lake Erie in 1943-62 with emphasis on contributions of the 1942-61 year-classes. J. Fish. Res. Board Can. 27:1475-1489.
- Parsons, J.W. 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. Trans. Amer. Fish. Soc. 100:474-485.
- Parsons, J.W., and J.B. Kimsey. 1954. A report on the Mississippi threadfin shad. Prog. Fish-Cult. 16:179-181.
- Patriarche, M.H., and R.S. Campbell. 1957. The development of the fish population in a new flood-control reservoir in Missouri, 1948 to 1954. Trans. Amer. Fish. Soc. 87:240-258.

- Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41:1825-1829.
- Pflieger, W.L. 1975. The fishes of Missouri. Mo. Dept. Conserv. 343 pp.
- Phillippy, C.L. 1964. Results of selective shad treatments in six central Florida lakes. Proc. Ann. Conf. S.E. Assoc. Game & Fish. Comm. 18:198-212.
- Price, J.W. 1963. A study of the food habits of some Lake Erie fish. Bull. Ohio Biol. Surv., New Ser. 2. 89 pp.
- Priegel, G.R. 1969. Age and rate of growth of the freshwater drum in Lake Winnebago, Wisconsin. Trans. Amer. Fish. Soc. 98:116-118.
- Priegel, G.R. 1971. Evaluation of intensive freshwater drum removal in Lake Winnebago, Wisconsin, 1955-1966. Tech. Bull. Wis. Dept. Nat. Resour. 47:28 p.
- Pritchard, A.L. 1929. The alewife (*Pomolobus pseudoharengus*) in Lake Ontario. Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab. 38:39-54.
- Radovich, J. 1979. Managing pelagic schooling prey species. pp. 365-375 in: H. Clepper, ed. Predator-prey systems in fisheries management. Sport Fishing Inst., Washington, D.C.
- Raleigh, R.F., D.H. Bennett, L.O. Mohn, and O.E. Maughan. 1978. Changes in fish stocks after major fish kills in the Clinch River near St. Paul, Virginia. Amer. Midl. Nat. 99:1-9.
- Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Amer. Fish. Soc. 108:505-529.
- Regier, H.A., and W.L. Hartman. 1973. Lake Erie's fish community: 150 yr of cultural stress. Science 180:1248-1255.
- Regier, H.A., V.C. Applegate, and R.A. Ryder. 1969. The ecology and management of the walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 15. 101 pp.
- Rhodes, R.J., D.A. Webb, and T.S. McComish. 1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. Proc. 17th Conf. Great Lakes Research, Intern. Assoc. Great Lakes Res.:593-595.
- Richkus, W.A. 1975. Migratory behavior and growth of juvenile anadromous alewives *Alosa pseudoharengus*, in a Rhode Island drainage. Trans. Amer. Fish. Soc. 104:483-493.
- Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.

- Ricker, W.E. 1962. Regulation of the abundance of pink salmon populations. pp. 155-201 in: N.J. Wilimovsky, ed. Symposium on pink salmon. Univ. British Columbia, Vancouver, B.C., Canada.
- Ricker, W.E. 1963. Big effects from small causes: Two examples from fish population dynamics. J. Fish. Res. Board Can. 20:257-264.
- Ricker, W.E. 1977. The historical development. p. 1-26 *in*: J. A. Gulland, ed. Fish population dynamics. J. Wiley & Sons. London.
- Ricker, W.E., and J. Gottschalk. 1940. An experiment in removing coarse fish from a lake. Trans. Amer. Fish. Soc. 70:382-390.
- Ricklefs, R.E. 1983. The economy of nature: a textbook in basic ecology. 2nd ed. Chiron Press, N.Y. 510 pp.
- Roff, D.A. 1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. 41:989-1000.
- Rose, E.T. 1957. Results of fish management at Blackhawk Lake. Iowa Conserv. Comm. Quart. Biol. Rep. 9:6-11. Cited in Miller (1960).
- Rose, E.T., and T. Moen. 1952. The increase in game-fish populations in East Okoboji Lake, Iowa, following intensive removal of rough fish. Trans. Amer. Fish. Soc. 82:104-114.
- Rosenthal, H., and D.F. Alderdice. 1976. Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae. J. Fish. Res. Board Can. 33:2047-2065.
- Rothschild, B.J. 1965. Aspects of the population dynamics of the alewife, *Alosa pseudoharengus* (Wilson), in Cayuga Lake, New York. Amer. Midl. Nat. 74:479-496.
- Rutledge, W.P., and J.C. Barron. 1972. The effects of the removal of stunted white crappie, *Pomoxis annularis* Rafinesque, on the remaining crappie population of Meridan State Park Lake, Basque County, Texas. Texas Parks Wildl. Dept. Tech. Bull. No. 12. 41 pp.
- Ryan, P.M., and H.H. Harvey. 1980. Growth responses of yellow perch, *Perca flavescens* (Mitchill), to lake acidification in the La Cloche mountain lakes of Ontario. Environ. Biol. Fishes 5:97-108.
- Rybicki, R.W., and K.H. Doan. 1966. Changes in the population of Lake Winnipeg whitefish. Fish. Branch, Man. Dept. Mines Nat. Resour., Winnipeg. 16 pp.
- Saville, A., and D. Schnack. 1981. Overview - some thoughts on the current status of studies of fish egg and larval distribution and abundance. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:153-157.

- Schmitz, W.R., and R.E. Hetfeld. 1965. Predation by introduced muskellunge on perch and bass, 11:yr 8-9. Wisconsin Academy of Sciences, Arts and Letters 54:273-282.
- Schneberger, E. 1935. Growth of the yellow perch (*Perca flavescens* Mitchill) in Nebish, Silver and Weber Lakes, Vilas County, Wisconsin. Trans. Wis. Acad. Sci., Arts & Letters 29:103-130.
- Schneider, J.C. 1973. Density dependent growth and mortality of yellow perch in ponds. Mich. Dept. Nat. Res., Fish. Res. Rep. 1795. 18 pp.
- Schneider, J.C., and J.H. Leach. 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great Lakes and possible causes, 1800-1975. J. Fish. Res. Board Can. 34:1878-1889.
- Schoffman, R.J. 1941. Age and growth of the drum in Reelfoot Lake. J. Tenn. Acad. Sci. 16:100-110.
- Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bull. 184. Fish. Res. Board Can. Ottawa, Ontario. 966 pp.
- Selgeby, J.H., W.R. MacCallum, and D.V. Swedberg. 1978. Predation by rainbow smelt (*Osmerus mordax*) on lake herring (*Coregonus artedii*) in western Lake Superior. J. Fish. Res. Board Can. 35:1457-1463.
- Shuter, B.J., and J.F. Koonce. 1977. A dynamic model of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) population. J. Fish. Res. Board Can. 34:1972-1982.
- Shuter, B.J., J.F. Koonce, and H.A. Regier. 1979. Modeling the western Lake Erie walleye population: A feasibility study. Great Lakes Fish. Comm. Tech. Rep. 32. 33 pp.
- Siler, J.R., W.J. Foris, and M.C. McInerney. in press. Spatial heterogeneity in fish parameters within a reservoir. in: G. E. Hall, ed. Reservoir fisheries management - strategies for the 80's, a symposium on managing reservoir fishery resources. Lexington, KY.
- Smith, P.E. 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v Réun. Cons. int. Explor. Mer. 173:117-127.
- Smith, S.H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25:667-693.
- Smith, S.H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Amer. Fish. Soc. 99:754-765.
- Smyly, W.J.P. 1952. Observations on the food of the fry of perch (*Perca fluviatilis*) in Windermere. Proc. Zool. Soc. Lond. 122:407-416.

- Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.
- Spangler, G.R. 1970. Factors of mortality in an exploited population of whitefish, *Coregonus clupeaformis*, in northern Lake Huron. pp. 515-529. in: C. C. Lindsey and C. S. Wood. Biology of coregonid fishes. University of Manitoba Press, Winnipeg, Manit.
- Spangler, G.R., and J.J. Collins. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37:2039-2046.
- Spangler, G.R., N.R. Payne, J.E. Thorpe, J.M. Byrne, H.A. Regier, and W.J. Christie. 1977. Responses of percids to exploitation. J. Fish Res. Board Can. 34:1983-1988.
- Stevens, R.E. 1964. Investigation of fish populations in Lakes Moultrie, Marion, Wateree, and Catawba, South Carolina. So. Carolina Wildl. Res. Dept., D-J Federal Air Proj. F-1-R-11, Combined Quart. - Ann. Prog. Rep. and Creel Census Completion Rep. Cited in Burns (1966).
- Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Amer. Fish. Soc. 110:751-763.
- Svardson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Rep. Inst. Freshwat. Res. Drottningholm 55:144-171.
- Swedberg, D.V. 1965. Age and rate of growth of freshwater drum, Lewis and Clark Lake, Missouri River. Proc. S. Dakota Acad. Sci. 44:160-168.
- Swedberg, D.V., and C.H. Walburg. 1970. Spawning and early life history of the freshwater drum in Lewis and Clark Lake, Missouri River. Trans. Amer. Fish. Soc. 99:560-570.
- Swenson, W.A., and L.L. Smith, Jr. 1976. Influence of food competition, predation and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota. J. Fish. Res. Board Can. 33:1946-1954.
- Swingle, H.S. 1949. Experiments with combinations of largemouth black bass, bluegills, and minnows in ponds. Trans. Amer. Fish. Soc. 76:46-62.
- Tarby, M. 1974. Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. Trans. Amer. Fish. Soc. 103:462-471.
- Theilacker, G.H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull. 76:403-414.

- Thorpe, J. 1977. Synopsis of biological data on the perch *Perca fluviatilis* Linnaeus, 1758 and *Perca flavescens* Mitchill, 1814. Food and Agric. Organ. United Nations, Fishery Synopsis 113.
- Torblaa, R.L., and R.W. Westman. 1980. Ecological impacts of lampricide treatments on sea lamprey (*Petromyzon marinus*) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37:1835-1850.
- Turner, W.R. 1953. The age and growth of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in Herrington Lake, Kentucky. Kent. Fish. Bull. 13. 14 p.
- Turnpenny, A.W.H., and R. Williams. 1981. Factors affecting the recovery of fish populations in an industrial river. Environ. Pollution Ser. A: 26:39-58.
- Van Oosten, J. 1937a. The age and growth of the Lake Erie sheepshead, *Aplodinotus grunniens* Rafinesque. Pap. Mich. Acad. Sci., Arts and Lett. 23:651-668.
- Van Oosten, J. 1937b. The dispersal of smelt, *Osmerus mordax* (Mitchill) in the Great Lakes region. Trans. Amer. Fish. Soc. 66:160-171.
- Van Oosten, J. 1947. Mortality of smelt *Osmerus mordax* (Mitchill), in Lakes Huron and Michigan during the fall and winter of 1942-1943. Trans. Amer. Fish. Soc. 74:310-337.
- Walburg, C.H. 1971. Loss of young fish in reservoir discharge and year-class survival, Lewis and Clark Lake, Missouri River. p. 441-448 in: G.E. Hall, ed. Reservoir fisheries and limnology. G.E. Hall, ed. Amer. Fish. Soc. Spec. Publ. 8.
- Walters, C.J., G. Steer, and G. Spangler. 1980. Responses of lake trout (*Salvelinus namaycush*) to harvesting, stocking, and lamprey reduction. Can. J. Fish. Aquat. Sci. 37:2133-2145.
- Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U. S. Fish. and Wildl. Serv. Fish. Bull. 67:1-15.
- Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. and Oceanogr. 15:556-565.
- Wells, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954-75. J. Fish. Res. Board Can. 34:1821-1829.
- Wells, L. 1985. Changes in Lake Michigan's prey populations with increasing salmonid abundance, 1962 to 1984. Paper presented to Great Lakes Fish. Comm., Lake Michigan Committee Meeting, Ann Arbor, MI, 20 March, 1985.

- Wells, L., and A.L. McLain. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29:889-898.
- Whillans, T.H. 1979. Historic transformations of fish communities in three Great Lakes Bays. J. Great Lakes Res. 5:195-215.
- Wickett, W.P. 1954. The oxygen supply to salmon eggs in spawning beds. J. Fish. Res. Board Can. 11:933-953.
- Wickliff, E.L. 1953. Gizzard shad rides again. Ohio Conserv. Bull. 17:23-25.
- Willis, D.W. 1984. Reproductive biology of gizzard shad in Melvern Reservoir, Kansas. Presented at 46th Midwest Fish & Wildlife Conf., Indianapolis, Ind.
- Wirth, T.L. 1958. Lake Winnebago freshwater drum. Wisconsin Cons. Bull. 23:30-32.
- Wolfert, D.R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. J. Fish. Res. Board Can. 26:1877-1888.
- Wrenn, W.B. 1968. Life history aspects of smallmouth buffalo and freshwater drum in Wheeler Reservoir, Alabama. Ann. Conf. S. E. Assoc. Game Fish. Comm. 22:479-495.
- Zeeman, E.C. 1976. Catastrophe theory. Sci. Amer. 234:65-83.

APPENDIX 1.

ANNOTATED BIBLIOGRAPHY

PAPERS INCLUDED IN ANNOTATED BIBLIOGRAPHY

Authors, date	Review Number
Alcorn, D. J., L. E. Fancher, and J. G. Moss 1980	24
Anderson, E. D., and L. L. Smith, Jr. 1971	31
Bagenal, T. B. 1977	40
Bardach, J. E. 1951	51
Beamish, R. J., and H. H. Harvey 1972	26
Beckman, W. C. 1941	1
Beckman, W. C. 1943	2
Beckman, W. C. 1950	3
Boaze, J. L., and R. T. Lackey 1974	36
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Burrough, R. J., P. R. Bregazzi, and C. R. Kennedy 1979	14
Burrough, R. J., and C. R. Kennedy 1979	13
Bury, R. B. 1972	25
Butler, R. L. 1965	47
Cada, G. F., and G. L. Hergenrader 1980	50
Chevalier, J. R. 1977	39
Clady, M. D. 1976	61
Craig, J.F., C. Kipling, E.D. LeCren, and J.C. McCormack 1979	60
Crunkilton, R. L., J. M. Czarnezki, and L. Trial 1980	34
Cushing, D. H. 1983	33
Deelder, C. L. 1951	59
Elwood, J. W., and T. F. Waters 1969	12
Eschmeyer, P. H. 1957	27
Eshenroder, R. L. 1977	62
Fraser, J. M. 1978	53
Grice, F. 1959	54
Gunning, G. E., and T. M. Berra 1968	16
Hanson, D. L., and T. F. Waters 1974	15
Healey, M. C. 1975	10
Healey, M. C. 1980	9
Higley, D. L., and C. E. Bond 1973	32
Holden, A. V. 1973	37
Holling, C. S. 1973	11
Jensen, A. L. 1981	43
Johnson, F. H. 1977	19
Johnston, C. E., and J. C. Cheverie 1980	17
Jones, D. D., and C. J. Walters 1976	44
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Kelso, J. R. M., and T. B. Bagenal 1977	55
Kenyon, R. B. 1978	42
Kneib, R. T. 1981	4
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Kushlan, J. A. 1974	30
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McFadden, J. T. 1977	46
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Priegel, G. R.	1971	49
Raleigh, R.F., D.H. Bennett, L.O. Mohn, and O.E. Maughan	1978	41
Ricker, W. E., and J. Gottschalk	1940	6
Rose, E. T., and T. Moen	1952	29
Ross, S. T., and J. A. Baker	1983	7
Ryan, P. M., and H. H. Harvey	1980	57
Spangler, G. R., and J. J. Collins	1980	8
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Turnpenny, A. W. H., and R. Williams	1981	21
Walters, C.J., G. Steer, and G. Spangler	1980	45
Wells, L.	1977	52

Beckman, W.C. 1941. Increased growth rate of rock bass, *Ambloplites rupestris* (Rafinesque), following reduction in the density of the population. Trans. Amer. Fish. Soc. 70:143-148.

Keywords: GROWTH, ROCK BASS, MIDWEST, EXPERIMENT, ROTENONE

Abstract: The fish of the south basin of Standard Lake were poisoned with rotenone. Samples of the rock bass population were taken at the time of the poisoning, in September, 1937. During 1939 and 1940 further collections were made in order to determine the effect of the population reduction. An increased growth rate, too great to be accounted for by any normal growth fluctuation, had occurred in fish of all ages.

Data and Review: Beckman poisoned 1/2 of the lake, which had stunted fish populations. He allowed the fish to freely move between basins and sampled rock bass 2 and 3 years after poisoning. There was a significant increase in growth rate observed after removal of 20,192 fish (3,155 fish/hectare; 24.5 kilograms/hectare) by poisoning (rotenone). Growth was measured as change in length. This was a clear demonstration of compensation by an increase in growth rate. No data were given on fecundity, post-poisoning population size, growth, etc.

Beckman, W.C. 1943. Further studies on the increased growth rate of the rock bass *Ambloplites rupestris* (Rafinesque), following the reduction in density of the population. Trans. Amer. Fish. Soc. 72:72-78.

Keywords: GROWTH, ROCK BASS, MIDWEST, EXPERIMENT, ROTENONE, CONDITION FACTOR, AGE-SPECIFIC GROWTH

Abstract: An increased growth rate, too great to be accounted for by any normal growth fluctuation, was shown to have occurred in all age-groups of rock bass, following the reduction in the population by poisoning the fish of the south basin of Booth (formerly called Standard) Lake, Michigan. Additional information was obtained in 1941 and 1942 which made it possible to analyze the change in growth in weight as well as length. Not only did the length and weight increase, but the mean coefficient of condition, K, also increased.

Data and Review: Continuation of Beckman (1941); two more years of data. There was little difference in the yearly growth increment (length) pre- and post-poisoning for age 1 fish; all other ages showed a significantly greater post-poisoning growth (increments nearly two times greater). The growth rate was approximately 3-5 g/yr before poisoning, with no appreciable variation with age. The growth rate after poisoning was approximately 11-64 g/yr and increased with age. The coefficient of condition was 3.07 pre-poisoning and

4.10 post-poisoning. Virtually the same paper as Beckman (1941), with a more extensive data set. Collections one whole year were done by fly fishing, which may bias size results.

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Beckman, W.C. 1950. Changes in growth rates of fishes following reduction in population densities by winterkill. Trans. Amer. Fish. Soc. 78:82-90.

Keywords: GROWTH, WINTERKILL, BLUEGILL, LARGEMOUTH BASS, YELLOW PERCH, PUMPKINSEED, MIDWEST

Abstract: Studies were made on four lakes in southern Michigan to determine the effect of the reduction in numbers of fish by winterkill upon the rate of growth of fishes. Earlier investigations on another lake had demonstrated that a severe reduction in population density had a marked effect on the rate of growth of the survivors. At the time of the winterkill in 1945 scale samples and counts of dead fish were obtained. Samples have been collected each year since the kill. An increase in the rate of growth too great to be accounted for by annual variations followed the winterkill in all but one species from one lake. The increase in growth rate was not maintained, however, for longer than a year in most species.

Data and Review: Beckman compared the growth (length) of four game fish species before and after a major winterkill in four lakes. The bluegill population in one lake was considered stunted prior to winterkill. All other populations were considered to be growing at about state average prior to winterkill. For five of the six populations studied, growth increased strongly the first year after winterkill, but then generally declined the second year after winterkill. In one lake, bluegill growth increased 35.6% in the first year after winterkill, over an average of the seven years before the winterkill. In another lake, bluegill growth increased 19.5% the first year and 29.0% the second year. Largemouth bass showed no increase in growth. Yellow perch growth in one lake increased 61.3% the first year, and decreased the second year. In another lake yellow perch increased 35.0% the first year and 32.7% the second year. Pumpkinseed growth was up 79.2% the first year, 15.5% the second year, and 39.1% the third year. (All percentages are compared to a seven year average before the kill.) In the last two cases (perch and pumpkinseed), bluegills were entirely killed off from that lake, which may account for the high growth rate of pumpkinseeds. Chubsuckers and yellow and brown bullheads were more abundant after winterkill than before. They may have been out-competing centrarchids and perch, and thus account for decreased growth rate of centrarchids and perch after a year or two. Rough fish showed less mortality from winterkill. Fish were collected by netting (no specifics given), hook and line, and subsequent minor winterkills. Methods were vague.

Kneib, R.T. 1981. Size-specific effects of density on the growth, fecundity and mortality of the fish *Fundulus heteroclitus* in an intertidal salt marsh. Mar. Ecol. Prog. Ser. 6:203-212.

Keywords: GROWTH, FECUNDITY, MORTALITY, MUMMICHOG, SIZE-SPECIFIC EFFECTS, DENSITY-DEPENDENT, EXPERIMENT, EAST

Abstract: Three size classes of *Fundulus heteroclitus* (L.) (small, 40-50 mm total length; medium, 50-69 mm TL; large, ≥ 70 mm TL) were maintained on an intertidal salt marsh in separate enclosures (10 m²) for 10 months at 3 densities (1, 2 and 4 ind./m²). During the final 6 weeks of the experiment (March-April 1979) the effects of density on individual growth as well as mortality and fecundity of the enclosed populations were assessed. Although fish density and growth were inversely related in all size classes, the growth rate of small *F. heteroclitus* remained positive even after 6 weeks at the highest experimental density. Medium size fish grew when enclosed at densities of 1 and 2 ind./m² but not at 4 ind./m². The growth of large fish was positive only in cages containing 1 ind./m². Over the range of experimental treatments, fecundity of medium size *F. heteroclitus* exhibited the strongest negative response to high density. However, the gonadosomatic index for large fish was lower than for either of the other size classes at all experimental densities, suggesting that fecundity of large individuals may be severely impaired even below the lowest density (1 ind./m²) used in the experiment. Density and fish losses (mortality + escape) were directly related only in the small and large fish size classes. After 6 weeks at a density of 4/m², 77% of the small fish and 60% of the large fish were lost compared to only 32% of the medium size individuals. Escape accounted for an estimated 13.2% of all losses and was independent of density. Total losses reflected a density-dependent trend in small and large fish mortality.

Data and Review: Kneib studied size-specific effects of density on individual growth, fecundity, and mortality of mummichog (*Fundulus heteroclitus*) in field enclosures in an intertidal marsh.

Major findings:

- 1) Growth (change in length) was inversely related to density. This was probably due to food limitation at high densities.
- 2) There was an inverse relationship between density and proportion of medium-sized females with ripe oocytes.
- 3) Significant density-dependent mortality was observed for small and large fish. The same trend was observed for medium-sized fish but was not significant.

This paper does not deal with catastrophic effects, but gives a good overview of density-dependent growth, fecundity, and mortality for mummichog. The methods are well documented.

Mahon, R., and M. Ferguson. 1981. Invasion of a new reservoir by fishes: species composition, growth, and condition. *Canadian Field-Naturalist* 95(3):272-275.

Keywords: BLUNTNOSE MINNOW, COMMON SHINER, CREEK CHUB, WHITE SUCKER, GROWTH, CONDITION FACTOR, IMPOUNDMENT, CANADA

Abstract: After the first summer of inundation, the ichthyofauna of the reservoir known as Guelph Lake (impoundment of Speed River) was compared to that of the Speed River before impoundment. Several species that had been rare in the river showed marked increases in relative abundance in the reservoir. The bluntnose minnow (*Pimephales notatus*) was most abundant among 19 species collected. For young-of-the-year of three species, bluntnose minnow, common shiner (*Notropis cornutus*), and creek chub (*Semotilus atromaculatus*), which were abundant enough for comparison, growth was faster in the reservoir than in the river. For these species and white sucker (*Catostomus commersoni*), the average condition (weight at a given length) was significantly higher in the reservoir.

Data and Review: The authors suggested that increase in growth may be due to increased food abundance but have no corroborating data.

Mean SL of young-of-the-year (in mm, presumably) in September:

Species	Impoundment	River
common shiner	36.4	29.4
creek chub	54.7	40.9
bluntnose minnow	33.3	27.6

Ratio of observed weight (from impoundment) to expected weight (from river): common shiner, 1.32; white sucker, 1.28; bluntnose minnow, 1.13; creek chub, 1.13. Sampled by 6-mm circular mesh seine, 18 stations.

Ricker, W.E., and J. Gottschalk. 1940. An experiment in removing coarse fish from a lake. *Trans. Amer. Fish. Soc.* 70:382-390.

Keywords: WALLEYE, WHITE BASS, SMALLMOUTH BASS, LARGEMOUTH BASS, BLUEGILL, PUMPKINSEED, YELLOW PERCH, BLACK CRAPPIE, EXPERIMENT, MIDWEST

Abstract and Review: Ricker extensively seined a 1,600-acre lake over a 2-year period (1935-1936) to remove rough fish (carp, quillback, buffalo, gar). Within one year after seining was initiated, there was a large increase in abundance of game fish accompanied by a decrease in turbidity and an increase

in macrophytes. Also observed was an increase in longnose and shortnose gar, species that were removed by seining; the authors attributed this, in part, to greater similarity in feeding habits between gar and game fish than with rough fish. This paper does not permit quantification of compensation in response to catastrophic reduction in densities. Interspecific competition may be the mechanism accounting for the increase in abundance.

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Ross, S.T., and J. A. Baker. 1983. The response of fishes to periodic spring floods in a southeastern stream. *Amer. Midl. Nat.* 109(1):1-14.

Keywords: SOUTH, FLOODING

Abstract: Movement of fishes onto a fringing floodplain was studied by seining and trapping during five spring floods. We collected 26 species from the inundated floodplain; the known channel fauna is 42 species. Species numerically dominant on the floodplain were *Fundulus olivaceus*, *F. notti*, *Gambusia affinis*, *Notropis welaka*, *N. texanus*, *N. roseipinnis*, *Lepomis macrochirus*, *L. cyanellus* and *L. marginatus*. A flood-exploitative species, *Notropis texanus*, had higher population abundance during 3 high-flow years than in 3 low-flow years, suggesting that spring flooding may exert significant control over fish community structure.

Data and Review: It was shown that abundances of some fish species (termed "flood exploiters") are positively correlated with spring flow. Increases in abundance apparently were not due to compensation; rather, flood exploiters apparently used abundant floodplain resources prior to spawning to increase energy available for reproduction.

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Spangler, G.R., and J.J. Collins. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. *Can. J. Fish. Aquat. Sci.* 37:2039-2046.

Keywords: LAKE WHITEFISH, SEA LAMPREY, GREAT LAKES, CANADA, SURVIVAL

Abstract: Changes in population parameters of three stocks of whitefish in Lake Huron following control of sea lamprey have varied between the major basins of the lake. In the North Channel and main basin, whitefish survival rates increased significantly, from values of 23 to 37% and 16 to 24%, respectively. In both areas the abundance of lamprey declined while whitefish increased. In Georgian Bay, whitefish populations did not reflect changes attributable to lamprey control, possibly because of low lamprey abundance. During the control period, whitefish survival rates declined from 57 to 39%, abundance declined and growth rates increased.

Data and Review: Population parameters of three whitefish stocks in Lake Huron were examined before and after lamprey control. In two basins where lamprey were abundant, whitefish increased after lamprey abundance declined. Whitefish survival rates increased greatly during this period. Total annual survival equaled 0.228 and 0.162 before lamprey control in two areas; 0.366 and 0.240 after, respectively. The paper did not show growth compensation. The results are consistent with basic predator-prey theory and not strongly applicable to compensation in response to catastrophic reduction in population size. The data were from commercial gill net catches.

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Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci. 37:255-267.

Keywords: LAKE WHITEFISH, GROWTH, AGE-SPECIFIC SURVIVAL, CANADA, EXPERIMENT

Abstract: From 1971 to 1978 Healey conducted an exploitation experiment on lake whitefish in four Northwest Territories lakes. Significant increases in size-at-age were recorded in the exploited lakes, and the degree and persistence of the increase were proportional to the intensity of exploitation. Good recruitment was stimulated on the heavily exploited lake, and to a lesser degree in the moderately exploited lake. Analyses of growth and year-class strength in the unexploited control lake and the lightly exploited lake indicated that natural variation in growth and recruitment, on a similar scale to that stimulated by exploitation, had occurred in the past. The compensatory responses of lake whitefish populations to exploitation appear to be a logical consequence of the natural population regulating mechanisms for the species. Results indicate that in unexploited lakes, recruitment and growth of young fish is regulated by the established population of mature fish.

Data and Review: This article also applies to non-catastrophic compensation. There were three degrees of exploitation in three lakes. The highest exploitation was approximately 50% of the population. The timing of samples was not explained much. Harvest samples were taken "summer and autumn"; Figure 2 (catch curve) shows the start of harvesting in 1973 and the end in 1974. The article does not say how many sampling times were in between, or what N is for each curve. Healey had a good control lake; he paid attention to control data. He held survey sampling of the control lake to 100 fish per year. Drygeese Lake was exploited at a maximum rate. At 30% exploitation per year for two years (total population reduced about 50%), seven of thirteen age classes showed significant increases in length. The average increase (all ages) was 12 mm (0-3 years after exploitation). After four years, four ages still were significantly longer than pre-exploitation. At Drygeese Lake, catches began to recover in the first year after exploitation. Mature fish were almost eliminated; ages 0+ and 1+ were very abundant during exploitation, and the abundance peak was still evident four years later. The discussion was

good; predation, catchability of young fish, and the influence of adults on young via behavior were discussed. Increased growth rate appeared to be the most important compensatory mechanism for lake whitefish.

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Healey, M.C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32:427-448.

Keywords: LAKE WHITEFISH, GROWTH, CANADA, GREAT LAKES, AGE AT MATURITY

Abstract: Available data on mortality, growth, reproduction, and stock size in exploited and unexploited populations of lake whitefish (*Coregonus clupeaformis*) are reviewed with a view to understanding the dynamics of exploited populations and improving their management. Natural mortality ranged from about 0.20 to 0.80 in unexploited populations. In exploited populations total mortality was as high as 0.94. Unexploited populations showed a wide range of growth rates. Growth rate increased with increasing exploitation, and growth rate in all heavily exploited populations was similar to the most rapid growth rate shown by unexploited stocks. Heavily exploited whitefish matured at a younger age and possibly also at a smaller size than those which were unexploited. Limited data on stock size suggest that although total population size declines under heavy exploitation, the vulnerable population remains of similar size.

It is concluded that whitefish respond to fluctuations in population size through compensatory changes in growth rate. The age difference between growth rate in a population and maximum growth rate is a measure of its scope for compensating for increased mortality. Populations with slow growth rate and low mortality should, therefore, have the best fishery potential, while those with high growth rate and high mortality have a low fishery potential. Further, it is possible to judge the fishery potential of a population or its stage of exploitation from relatively simple measurements of mortality, growth, age structure, and maturity.

Data and Review: This is a literature review. Most of the examples are for unexploited or constantly exploited populations, and are not catastrophic. Mortality was so variable for lake whitefish that evidence of compensatory mortality was not found. The fishery collapse example in Miller (1947) was discussed here and will also be reviewed. There was much evidence for compensatory growth. Figure 4, page 437 shows growth rates of many populations exploited to different degrees. Limited data suggested that age at maturity is younger and size at maturity smaller for exploited populations. Healey believed fecundity is probably not compensatory in lake whitefish.

Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Systematics 4:1-23.

Keywords: REVIEW, MODELING, STABILITY, RESILIENCE, LAKE TROUT

Abstract: Holling discusses traditional models and the factors that make them different from real ecosystems. Examples of different system behaviors are shown. More than one discrete domain of attraction (local stability, spiraling in from certain starting points) may exist for a given system. Freshwater aquatic systems are approximately self-contained, homogeneous, with small climatic fluctuations. In such systems, fishing pressure, environmental change, or appearance of exotics may set conditions for population collapse by reducing resilience of the system, as with lake trout in Lake Michigan. Stability is the ability of a system to return to equilibrium after a temporary disturbance. Resilience is a measure of the persistence of the system and its ability to absorb change or disturbance and still maintain the same relationships between populations or state variables. An unstable system may be highly resilient.

Data and Review: Few data are given, as this is a review paper. The paper gives good explanations of traditional models and their shortcomings. It discusses Great Lakes examples in terms of the theory involved, characterizing them as stable, non-resilient systems which can easily go "over the edge" to another domain of attraction (e.g. lake trout-bloater complex to alewife-smelt-perch or exotics). The paper cites Smith (1968) and Beeton (1969). Lake Michigan was affected by fishing pressure, eutrophication, physical changes, a foreign predator (sea lamprey), and foreign competitors (alewife and carp). A precondition for lake trout collapse was set by the harvesting of fish, which reduced resilience of the system so when lamprey appeared (unexpected event), the population collapsed. If it had not been the lamprey, something else would have destroyed lake trout populations: climate change, environmental change, or species composition change. It should be possible to determine, from lake trout history, the boundary population below which they cannot compensate.

Elwood, J.W., and T.F. Waters. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. Trans. Amer. Fish. Soc. 98:253-262.

Keywords: BROOK TROUT, FLOODING, MIDWEST, GROWTH

Abstract: Food consumption and production rates were estimated for a stream population of brook trout, *Salvelinus fontinalis* Mitchill, over a two-year period (1965-1966) in which four severe floods occurred. Two year classes were nearly eliminated as producing components of the population. Standing

crops of older age-groups were reduced as a result of a decrease in the stream's carrying capacity after sand and debris, carried into the stream by flood waters, filled pools and blanketed riffle areas.

Data and Review: Elwood and Waters followed the brook trout population in a small stream before, during, and slightly after a series of severe floods. Unfortunately, there are insufficient pre- and post- flood data to say much about compensation. Floods reduced the population from about 6,500 fish/hectare to <500/hectare by the end of the study. It appeared that post-flood growth rates were greater than pre-flood rates because total standing crop began to increase after the flood even though population density continued to decline. Weight over time for two year classes was graphed. Year classes look quite different but numbers were not given and statistical tests were not done. The collection method was electrofishing. Age was calculated by scale reading.

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Burrough, R.J., and C.R. Kennedy. 1979. The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). J. Fish Biol. 15:93-109.

Keywords: ROACH, PARASITISM, ENGLAND, GROWTH, FECUNDITY, SIZE AT MATURITY, CONDITION FACTOR

Abstract: Two sudden and pronounced changes in the growth rate of roach, *Rutilus rutilus* (L.), in Slapton Ley, Devon, were observed between 1972 and 1976. At first the growth rate declined to the point at which the population became stunted, then subsequently it improved again. These changes were correlated with population density; the numbers of roach were increasing during the late 1960s/early 1970s, and this increase was substantially reinforced by very strong year classes in 1972, and, to a lesser extent, in 1973. The increase in population density resulting from the strong 1972 year class was apparently adequate to accelerate the onset of the stunting observed. The improvement in growth rate in 1976 followed immediately after extensive mortalities amongst the roach during 1975, caused by an epidemic of the parasite *Ligula intestinalis* (L.). Some improvement in the growth of age-0 roach had been evident during 1975, but this was not observed in the population. Ford-Walford plots showed a decline in the value of L_{∞} (theoretical ultimate length) after the onset of stunting in 1972.

Differences in the reproductive biology of the fish were found following the alleviation of stunting; the gonads of both sexes achieved a greater relative weight, and correspondingly the fecundity of the females was higher, although this latter effect became progressively less marked with increasing size. It was not apparent amongst the largest individuals. There was also some evidence of a decline in the proportion of fish maturing at minimum size. The changes in reproductive biology were associated with the improvement in conditions for individual fish following the decline in population density.

Data and Review: The methods of collection were seine, gill net, electrofishing, and traps. Thirty fish were taken each month. Some bias in favor of larger fish was known and stated by the authors. Methods were fairly standard. Scales were used for aging. Back-calculated growth was done by posterior scale radius. Most mortality due to parasitism occurred in a single year; the following year, growth rate, relative condition, and gonad weight/total body weight all increased substantially. Relative growth in length increased from 58.6% in 1975 (the year of large mortality) to 191.7% in 1976. Weights for each age-group, 1 to 4, more than doubled from 1975 to 1976. Condition factor did not drop dramatically after spawning in 1976 as it had in 1975. There was significantly greater fecundity in 1976, but means were not given, only regression parameters. Size at maturity was given as 80-90 mm for males and 90-100 mm for females, but it was not clear which year. Fish were slightly larger in 1976, due to growth; age at maturity was probably the same.

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Burrough, R.J., P.R. Bregazzi and C.R. Kennedy. 1979. Interspecific dominance amongst three species of coarse fish in Slapton Ley, Devon. J. Fish Biol. 15:535-544.

Keywords: ROACH, RUDD, EURASIAN PERCH, ENGLAND, COMPETITION

Abstract: Marked changes in the relative numbers of roach *Rutilus rutilus* (L.), rudd *Scardinius erythrophthalmus* (L.) and perch *Perca fluviatilis* L., in Slapton Ley, Devon, have been observed over the period 1967-1978. Historically, the lake had been dominated by rudd and perch; significant numbers of roach were not thought to be present until 1967. From then onwards the roach population exhibited a considerable expansion, apparently replacing the rudd, which had virtually disappeared by 1974. In 1975 extensive mortalities of roach were caused by the pseudophyllidean cestode *Ligula intestinalis* L. During 1976 and 1977 larger numbers of rudd, belonging to the 1975 and 1976 year classes, were present, suggesting that the roach mortalities might be giving the rudd a chance to recover. However, very few rudd were present during 1978, possibly because lower incidences of ligulosis during 1976-1978 had allowed the roach to recover from the main outbreak of the disease in 1975, and to replace the rudd for the second time. Evidence from trap catches indicated that the perch population had shown a consistent decline between 1970 and 1977. The major phase of this decrease occurred between 1971 and 1973, when the roach population was increasing the most rapidly. Comparisons were made with changes in fish populations in other localities. The major reason for the changes observed was thought to be a competitive relationship between the plankton feeding younger stages, with roach being the dominant species, although other factors may also have been involved.

Data and Review: All the data given concern relative abundance of the three species. We cannot derive degree of compensation or pin down the mechanisms. Roach may be at a competitive advantage in eutrophic situations, and Slapton

Ley has become more eutrophic in recent years. Habitat change and faster growth of juvenile roach than of rudd may have provided a competitive advantage.

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Hanson, D.L., and T.F. Waters. 1974. Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. Trans. Amer. Fish. Soc. 103:431-439.

Keywords: BROOK TROUT, FLOODING, MIDWEST, GROWTH

Abstract: The brook trout (*Salvelinus fontinalis* Mitchill) population in Valley Creek, Minnesota, recovered from heavy flood damage in 1965-66 in terms of standing crop, growth, and production rates over a period of 4 to 5 years. Standing crops of brook trout increased numerically by 20-fold from a low of 498/ha in 1966 to 10,882/ha in 1969, and in biomass by 6-fold from 25 kg/ha in 1966 to a maximum of 148 kg/ha in 1970. Growth rate early in the recovery period was high due to the low density of trout but decreased in successive years as fish density increased.

Data and Review: This paper is a continuation of a study by Elwood and Waters (1969). It follows the recovery of a brook trout population in a small stream after the population had been severely reduced by floods. The population recovered to pre-flood levels within three years after the flood but standing crop biomass did not return to pre-flood levels. Growth rates were high for about 2 years after the floods and then declined, but pre-flood growth rates were not available for comparison. The only really notable high growth was age 0 of the 1966 year class (immediately after the floods). Mean weight of age 0 that year was 20.0 g, compared to 7.5 g in 1965 and 8.1 g in 1967. The 1965 and 1966 year classes were virtually eliminated by floods. Post-flood brook trout production in the stream was high, at the upper end of the range of salmonid streams worldwide; again, pre-flood production estimates were not given.

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Gunning, G.E., and T.M. Berra. 1968. Repopulation of a decimated stream segment by the sharpfin chubsucker. Prog. Fish-Cult. 30:92-95.

Keywords: SHARPFIN CHUBSUCKER, EXPERIMENT, STREAM, SOUTHEAST, IMMIGRATION

Abstract: Sharpfin chubsuckers (*Erimyzon tenuis*) were decimated by electroshocking in a 33-m section of Talisheek Creek, Louisiana. Forty-one individuals were removed from June 9, 1966 to March 2, 1967. Twenty-six were taken July 10-12, 1967, compared to fifteen in the 1966 sample of like effort. The 1967 sample had higher mean weight and mean total length than the 1966 sample. Repopulation was accomplished by immigration of juvenile sharpfin chubsuckers.

Data and Review: Little information is given on compensation. The paper documents immigration of sharpfin chubsucker into a stream segment where chubsuckers had been removed by electrofishing. The average weight and length were greater for the repopulation sample but variation looks high. No statistics were done.

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Johnston, C.E., and J.C. Cheverie. 1980. Repopulation of a coastal stream by brook trout and rainbow trout after endosulfan poisoning. Prog. Fish-Cult. 42:107-110.

Keywords: BROOK TROUT, RAINBOW TROUT, TOXIC SPILL, NORTHEAST, IMMIGRATION, STREAM

Abstracts: A 905-m section of North Brook, Prince Edward Island, contained an estimated 246 to 456 brook trout (*Salvelinus fontinalis*) and 5 to 27 rainbow trout (*Salmo gairdneri*) per 100 m of stream before an accidental spill of the chlorinated hydrocarbon, endosulfan, in August 1975 killed all fish in the section. Small numbers of brook trout were observed in North Brook in the fall of 1975. Populations in June 1976 were estimated to be 135 brook trout and 10 rainbow trout per 100 m of stream. Nearly the entire population was made up of emigrants from areas unaffected by the endosulfan. Natural reproduction in the study area was insignificant during the first year after the fish kill.

Data and Review: This paper is similar to Gunning and Berra (1968). The authors speculated that toxic residues may have adsorbed on sediment surfaces and affected egg survival. The paper may demonstrate inability to compensate.

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Olmsted, L.L., and D.G. Cloutman. 1974. Repopulation after a fish kill in Mud Creek, Washington County, Arkansas following pesticide pollution. Trans. Amer. Fish. Soc. 103:79-87.

Keywords: TOXIC SPILL, SOUTH, IMMIGRATION, STREAM

Abstract: Repopulation after a fish kill caused by pesticide pollution in Mud Creek, Washington County, Arkansas is reported. Twenty-nine species of fishes were eliminated from the study area as a result of the poison. Repopulation began almost immediately after the pesticide dissipated, and was accomplished primarily by immature individuals. Chronology and rate of repopulation of each species are reported, and factors influencing the rate of repopulation and population structure are discussed.

Data and Review: This study is similar to Gunning and Berra (1968). No information is given on compensation.

Johnson, F.H. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. 34:1633-1642.

Keywords: WHITE SUCKER, WALLEYE, YELLOW PERCH, EXPERIMENT, MIDWEST, COMPETITION, AGE-SPECIFIC SURVIVAL, GROWTH, CONDITION FACTOR

Abstract: In a northeastern Minnesota lake subject only to sport fishing, removal of 85% of the estimated standing crop (34 kg/ha) of adult white suckers, *Catostomus commersoni*, in 1966 was followed by marked changes in community structure and interrelations. During 7 years after the removal: catch indices for adult suckers remained far below those before the sucker removal but juvenile suckers increased about 17-fold; yellow perch, *Perca flavescens*, increased about 15-fold; walleye, *Stizostedion vitreum vitreum*, standing crop increased about one-third; young-of-the-year perch increased in diet of adult walleye; walleye angling yield increased from an average of 3.0 kg/ha before the removal to an average of 4.9 kg/ha in 1970-73; the rate of exploitation of adult walleye did not change with increase in angling effort; and the increased walleye harvest consisted mostly of fish recruited to the catch during the fishing season. The average annual harvest of walleye in 1970-73 exceeded estimated potential production for all fish by 81.5% and probably cannot be sustained. Removal of white suckers from lakes with limited fish species diversity appears to benefit percid populations.

Data and Review: Johnson gave relative abundance data on young-of-the-year white sucker, yellow perch, and walleye. The data imply increased survival of young of all three species after sucker removal, but survival rates can't be obtained from the data. Growth rates of immature white suckers (ages 1-4) were greater after sucker removal, but this was only significant for age 3 fish ($P < 0.05$). Abundance of young was high 3 years after removal, with the population increasing rapidly 5-7 years after removal. Yellow perch young were abundant 2 years after sucker removal. Mean annual growth increment was 10 mm greater from age 1 to 2 and age 2 to 3 after sucker removal. Growth declined again as abundance increased. Yellow perch condition factor increased from 1.06 before sucker removal to 1.24 the following year. Walleye growth was generally faster for five years following sucker removal (no data given). Condition factor of male walleye > 460 mm was slightly higher 3-6 years after sucker removal ($K = 0.91$) than before sucker removal (0.87), but declined 7 years after removal. Walleye < 460 mm showed no increase in condition factor after sucker removal. A strong walleye year class was produced 4 years after sucker removal.

This paper demonstrates compensation but does not give the detailed data necessary to quantify all mechanisms mentioned. Johnson (1975), cited in this paper, may give more data. Depth or substrate of stations may affect catch for these species, but sampling stations are not described, so they cannot be evaluated. Otherwise the methods seem appropriate. The conclusions may not have general applicability to more complex systems; this lake has few species.

Torblaa, R.L., and R.W. Westman. 1980. Ecological impacts of lampricide treatments on sea lamprey (*Petromyzon marinus*) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37:1835-1850.

Keywords: SEA LAMPREY, GREAT LAKES, POISONING, GROWTH, SEX RATIO

Abstract: Abundance of ammocoetes and transformed individuals has declined in most watersheds with a few exceptions where density-dependent factors may have been influential. Increased growth was related to reduced density. Sex compositions of larval and metamorphosing populations were highly variable during initial lampricide treatments. Females predominated in some streams, males in others. Streams once dominated by males now favor females in residual and reestablished populations of larvae. The shift to femaleness in the larval populations has precipitated a similar shift in adult sea lamprey populations of the upper Great Lakes.

Data and Review: In Great Lakes tributaries, sea lamprey ammocoetes of year-classes established after treatment with TFM or Baker 73 grew faster than succeeding year-classes; as density increased, growth rate declined. No original growth data are given for ammocoetes. Greater growth of transformed sea lampreys following TFM treatment was also observed; mean length increased from 143 mm during the first treatment to 157 mm during the second treatment. Most growth information in this paper is apparently from Purvis (1979), cited in this paper. For Lakes Superior and Huron tributaries, where males predominated before treatment, percentage males decreased significantly after treatment (χ^2 test, $P < 0.001$), showing sex ratio compensation (more females when densities lower). In tributaries where females dominated before treatment, sex ratios usually remained about the same. Lake Ontario tributaries did not show as clear results. Streams that were predominately male before treatment all had high densities of larvae, also indicating density-dependence of sex ratio. Percent males decreased from 72 to 15% in the Michipicoten River during 5 treatments, one of the more striking examples. Many sex ratio data are given in tables and figures for adults and ammocoetes.

Turnpenny, A.W.H., and R. Williams. 1981. Factors affecting the recovery of fish populations in an industrial river. Environmental Pollution (Series A) 26:39-58.

Keywords: BROWN TROUT, BRITAIN, GROWTH, CONDITION FACTOR, TOXICS, POLLUTION

Abstract: The River Ebbw Fawr, an industrial river of southeast Wales, was investigated over a three-year period to follow the re-establishment of fish populations as a result of pollution control measures at coal washeries and a steelworks on the river. Five freshwater fish species became established in parts of the river during the study period (1974-77). The brown trout *Salmo*

trutta L. was the first to enter. Good growth and condition factors among the recolonizing brown trout stock suggest that a sport fishery could be developed on the river.

Data and Review: Little useful information is given on compensation. This paper follows reestablishment of fish populations in a river after effective pollution control was established. It shows that recolonizing fish have high growth rates and high condition factor in comparison with fish in similar, non-polluted streams. No natural reproduction was taking place in the river (excessive silt in gravel). No data were given on fish populations prior to and/or during pollution.

22

Kohler, C.C., and J.J. Ney. 1981. Consequences of an alewife die-off to fish and zooplankton in a reservoir. Trans. Amer. Fish. Soc. 110:360-369.

Keywords: ALEWIFE, SOUTHEAST, INTERSPECIFIC AND INTRASPECIFIC COMPETITION, WINTERKILL, GROWTH

Abstract: Alewife *Alosa pseudoharengus* was the principal pelagic forage species in Claytor Lake, Virginia, prior to a severe die-off in the winter of 1977-1978. Due to successful reproduction in 1978, abundance of alewives rebounded sharply in 1979. Alewife-induced shifts in zooplankton composition toward smaller forms represent a potentially significant adverse impact on cohabiting planktivores, including young-of-the-year sport fishes. Growth of adult alewives and young-of-the-year walleyes and white bass was significantly greater in 1978 than in the 2 years preceding the die-off, suggesting that both intra- and interspecific trophic competition operate when alewife density is high. Annual growth of age-2 walleyes and white bass did not differ substantially before and after the die-off; impact of the population collapse may have been mitigated by high reproductive success and rapid first-year growth of alewives in 1978. These findings indicate that alewife size-selective planktivory may have a more enduring and potentially severe impact on the reservoir fishery than does instability in the alewife population.

Data and Review: Kohler and Ney examined age-specific growth rates of alewives in a reservoir before and after a die-off. The growth rate (annual increment in total length) was significantly greater after the die-off for age 2 and 4 alewives and marginally greater ($P=0.10$) for age 3 fish; growth rates for age 1 fish were nearly identical before and after the die-off. Age structure of the population before and immediately after the die-off was not given.

23

Keleher, J.J. 1972. Great Slave Lake: effects of exploitation on the salmonid community. J. Fish. Res. Bd. Canada 29:741-753.

Keywords: LAKE TROUT, LAKE WHITEFISH, CISCO, CANADA

Abstract: A 20-year investigation commenced at the inception of the Great Slave Lake commercial fishery, and it is inferred that exploitation has been the sole cause of change in the fish stocks. Lake whitefish, *Coregonus clupeaformis*, and lake trout, *Salvelinus namaycush*, have made up 94% of the commercial landings of 54 million kg during the period. The annual catch of these two species rose from 0.7 million kg in 1945 to a maximum of 4 million kg in 1949 then gradually decreased to about the 2 million kg level. The average size of commercially caught fish has declined to about 0.9 kg for whitefish and 2.2 kg for trout. Information on catch per unit effort for other species indicates no evident explosions in their numbers, though ciscoes, *Leucichthys* spp., appear to have increased in abundance.

Data and Review: Keleher reviewed the 20-year history of commercial fishing exploitation on fish stocks in Great Slave Lake. Virtually no information is given on compensation.

24

Alcorn, D.J., L.E. Fancher, and J.G. Moss. 1980. Harbor seal and fish populations - before and after a sewage spill in south San Francisco Bay. Calif. Fish and Game 66:238-240.

Keywords: PACIFIC COAST, SPILL

Abstract: A sewage spill occurred 4 through 29 September 1979, at the San Jose-Santa Clara Water Pollution Control Plant, during which 15 billion liters of partially treated sewage flowed into Artesian Slough. Obvious short-term effects of the sewage spill on nearby Mowry Slough seal and fish populations appear to be minimal or absent. Long-term effects are possible and monthly monitoring of both seal and fish populations continues.

Data and Review: The sewage spill had no detectable impact on fish or harbor seal populations. No information is given on compensation.

25

Moring, J.R. 1981. Changes in populations of reticulate sculpins (*Cottus perplexus*) after clear-cut logging as indicated by downstream migrants. Amer. Midl. Nat. 105:204-207.

Keywords: RETICULATE SCULPIN, NORTHWEST, LOGGING, GROWTH

Abstract: Downstream movements of reticulate sculpins *Cottus perplexus* were monitored for 7 years before and 7 years after clear-cut logging of a watershed of a tributary of the Alsea River, Oregon. Short-term decreases in populations, as indicated by reduced numbers of migrating fish, persisted for 5 years. During this period, the average length of the sculpins remained significantly higher than before, possibly indicating a reduction in competition. Timing of downstream movements did not change.

Data and Review: Moring compared the number and size (total length) of reticulate sculpins moving downstream annually in two small streams before and after the entire watershed of one of the streams had been clearcut. The sculpin population was greatly reduced in the clearcut stream; the two youngest year classes were apparently eliminated immediately after clearcutting (Krohn 1968 cited in this paper). Population size (as evidenced by number fish trapped moving downstream) remained low in the clearcut stream for 7 years post-logging, and the average total length of fish in the population increased post-logging in the clearcut stream, but not in the control stream. This size increase could be due to compensatory growth (as the author suggested) or simply due to a change in the size structure of the population. Since small fish were most strongly affected by the logging, the latter explanation seems most parsimonious. Age-specific growth rates would be needed to determine if this is a good example of compensation.

26

Beamish, R.J., and H.H. Harvey. 1972. Acidification of the La Cloche Mountain Lakes, Ontario, and resulting fish mortalities. J. Fish. Res. Bd. Canada 29:1131-1143.

Keywords: LAKE TROUT, LAKE HERRING, WHITE SUCKER, YELLOW PERCH, CANADA, ACIDIFICATION, REPRODUCTIVE FAILURE

Abstract: The loss of populations of lake trout (*Salvelinus namaycush*), lake herring (*Coregonus artedii*), white suckers (*Catostomus commersoni*), and other fishes in Lumsden Lake was attributed to increasing levels of acidity within the lake. An absence of fishes was also observed in nearby lakes. In some lakes, acid levels have increased more than one hundredfold in the last decade. The increases in acidity appear to result from acid fallout in rain and snow.

Data and Review: This paper documents virtual elimination of game and non-game fish populations in Lumsden Lake over a ten-year period (1961-1971) in which all of the lakes in the La Cloche Mountain Lakes became highly acidic (pH between 4 and 5 in most lakes). Yellow perch were eliminated. The study does not provide any information on compensation. Acidification is severe and ongoing, thus fish cannot recover or compensate.

27

Eschmeyer, P.H. 1957. The near extinction of lake trout in Lake Michigan. Trans. Amer. Fish. Soc. 85:102-119.

Keywords: LAKE TROUT, GREAT LAKES, PREDATION, OVERFISHING

Abstract: After the collapse of the commercial fishery for lake trout (*Salvelinus namaycush*) in Lake Michigan in the late 1940s, the further decline of the population was traced by records of numbers of small lake trout (mostly

28 to 41 cm in total length and 3 to 5 years old) caught in small-mesh nets of the chub (*Coregonus* spp.) fishery. By 1951 the estimated abundance of these lake trout in lower Lake Michigan was only about 4% of their abundance prior to the invasion of the sea lamprey (*Petromyzon marinus*). This remnant of the population declined severely in subsequent years to a point near extinction by 1955. In April-July 1955 only eight lake trout were caught in 1.7 million m of gill net. Lake trout were brought near extinction by lethal attacks of the sea lamprey and by the near or perhaps complete failure of natural reproduction in 1949 and subsequently.

Data and Review: This paper describes the decline of lake trout in Lake Michigan through 1955. The only information remotely related to compensation concerns the size distribution of lake trout taken in chub nets (small-mesh nets) between 1951 and 1955 in southeastern Lake Michigan; percent of legal-sized lake trout in chub nets increased from 5% (n=1,113) in 1951 to 75% (n=4) in 1955. The author argued that this is evidence for reproductive failure (and it most likely is), but compensatory growth could also have occurred.

28

Mortensen, E. 1977. Density-dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams. J. Fish Biol. 11:613-617.

Keywords: BROWN TROUT, EUROPE, STREAM MODIFICATION, DENSITY-DEPENDENT MORTALITY

Abstract: The natural mortality rate of trout fry and the impact of weed cutting and cleaning out of weeds, branches and twigs from the stream-bed upon the mortality rate of trout fry was studied on several reaches in small streams. Above an initial density of 3.1 fry/m² natural mortality rate was found to be density-dependent in the first few months of life. In reaches where weed cutting and cleaning out of the stream-bed had taken place the mortality rate was higher than that found under natural conditions in undisturbed reaches.

Data and Review: Populations of brown trout were followed for the first several months after emergence in several small Danish streams. Fry mortality in undisturbed stream reaches was compared to two reaches (in different streams) where weeds were cut and weeds, branches, twigs, and larger stones were removed from the stream bed. In undisturbed reaches, fry mortality was density-independent at low initial densities (<3 fry/m²) and density-dependent at initial densities >3 fry/m². Daily instantaneous mortality rates were considerably greater in disturbed reaches (~0.018) than in undisturbed reaches (~0.012) at comparable initial fry densities. Since these trout populations appeared to be regulated by density-dependent mechanisms, follow-up studies in disturbed streams would be interesting in showing if and how stream trout populations compensate for increased fry mortality. This paper shows density-dependent mortality, but unrelated to the catastrophe.

Rose, E.T., and T. Moen. 1952. The increase in game-fish populations in East Okoboji Lake, Iowa, following intensive removal of rough fish. Trans. Amer. Fish. Soc. 82:104-114.

Keywords: YELLOW PERCH, WALLEYE, CENTRARCHIDS, BLACK BULLHEAD, MIDWEST, WINTERKILL, COMPETITION, RECRUITMENT

Abstract and Review: An effort was made to remove rough fish (largely bigmouth buffalo *ictiobus cyprinellus*, carp, and freshwater drum) from East Okoboji Lake, Iowa, from 1940 to 1951 using seines and traps. Game fish populations (catch per seine haul using a 762-m, 6.4-cm-mesh drag seine) were monitored throughout the 12-year rough fish removal period. Game fish (total of eight species) per seine haul increased from an average of 89 (27 kg) in 1940 through 1945 to an average of 1,100 (254 kg) in 1947 through 1950. [A winter kill in 1950-1951 greatly reduced catch per unit effort in the spring-summer of 1951 for both game and rough fish. But catch of YOY walleye and yellow perch increased noticeably after the winterkill: to 196 and 5,383 respectively compared to average of 7 and 97 for 1940-1945.] Not all game fish increased in response to the rough fish removals. CPUE of young-of-the-year and older northern pike, walleye, largemouth bass, and white bass did not change significantly over the 12-year period (except for walleye after the winterkill). Yellow perch, crappie, bluegill, and black bullheads showed significant increases in young-of-the-year and older fish in the years following 1945. The species that did not respond to the rough fish removal are all relatively large piscivores. These species probably do not compete with the rough fish for resources (especially food), which helps to explain why their densities did not change in response to rough fish removal. Release from competition is the most likely explanation for the increase in the other game fish species, but improvements in habitat quality (e.g., reestablishment of weed beds and the elimination of blue-green algal blooms) and, perhaps, concomitant changes in carrying capacity undoubtedly also played a role.

Kushlan, J. A. 1974. Effects of a natural fish kill on the water quality, plankton, and fish population of a pond in the Big Cypress Swamp, Florida. Trans. Amer. Fish. Soc. 103:235-243.

Keywords: DEWATERING, SOUTHEAST, OXYGEN

Abstract: A naturally occurring fish kill took place during the southern Florida dry season when receding water levels forced aquatic organisms out of shallow swamps and into a small pond. The fish kill had no effect on the long-term limnological characteristics of the pond, as water quality returned to normal range within 2 months and phytoplankton disappeared within 1 month after the fish kill. The species of fish in the pond showed a range of susceptibility to low oxygen concentration and other aspects of the fish kill.

Data and Review: This paper documents the occurrence of a massive natural fish kill in a Florida pond at the end of the dry season in 1970. Fish occurring in Big Cypress Swamp became concentrated in isolated ponds due to declining water levels during the dry season. The fish kill in the pond studied occurred when dissolved oxygen concentrations fell to nearly 0 ppm (<1 ppm at 1 cm depth; 0 ppm throughout the rest of the water column). This particular study has little value concerning compensation because it is only concerned with which species were eliminated during the kill, which species survived, and how some species were able to survive the low DO concentrations. A follow-up study, if available, could contain valuable information as this was certainly a good case of a catastrophic reduction in fish populations (99.4% of the total fish population in the pond died during the fish kill).

31

Anderson, E.D., and L.L. Smith, Jr. 1971. Factors affecting abundance of lake herring (*Coregonus artedii* Lesueur) in western Lake Superior. Trans. Amer. Fish. Soc. 100:691-707.

Keywords: LAKE HERRING, GREAT LAKES, OVERFISHING, INTERSPECIFIC COMPETITION, GROWTH, CONDITION FACTOR, FECUNDITY

Abstract: A field and laboratory study was conducted in 1965-1968 to investigate factors affecting lake herring (*Coregonus artedii* Lesueur) abundance in western Lake Superior. Commercial landings in November-December in the Duluth-Superior area dropped from 502,650 kg in 1954 to 900 kg in 1966. Wisconsin catches also declined markedly. Abundance and fishing intensity indices decreased with landings. Commercial catches and abundance of chubs (*Coregonus* spp.) and smelt (*Osmerus mordax*) increased simultaneously with the herring reduction. Average age of adult herring in commercial catches increased from 3.9 years in 1950-1959 to 5.1 in 1966-1968 but showed no significant difference between areas. Percentage of females did not show a trend from 1960 to 1968; however, the 1968 percentage of 85.0 was the greatest since 1962. Percentage of females increased with age. Average length and weight increased from 287 mm and 148 g in 1950-1959 to 340 mm and 301 g in 1966-1968. Average number of eggs per gram of fish increased from 30 in 1950-1954 to 39 and 36 in the Duluth-Superior and Apostle Islands areas, respectively, in 1966-1967. Smelt was the most abundant species in both areas and more abundant at Duluth-Superior. Correlations between fishing intensity and herring abundance suggest that overfishing was not the major factor in the decline of the species. Predation was not found to be a serious influence on herring. Food of herring, bloaters (*Coregonus hoyi*), and smelt was quite similar during early stages. Food similarities and highly significant negative correlations between herring and bloater abundance and herring and smelt abundance suggest that competition for food at the critical larval stage was likely the major influence in the lake herring decline.

Data and Review: Lake herring abundance in western Lake Superior declined drastically between 1954 and 1966 due to overfishing and interspecific competition. Anderson and Smith believed competition for food between lake

herring, chub (bloaters) and smelt was largely responsible for the decline; competition was likely most intense between larvae and may have helped to account for declining recruitment while fecundity is increasing. Based on the data, the authors' conclusion that competition is largely responsible for the decline is certainly debatable. Rather, overfishing of lake herring may have permitted the other species to increase. Mean age of the population (3.9 yr in 1950-1959) increased as population size decreased (5.1 yr in 1966-1968) indicating a decline in recruitment over the period. Size of herring increased as population size decreased.

1950-1954 mean length 287 mm; mean weight 148 g.

1956-1961 mean length 305 mm; mean weight 207 g.

1966-1968 mean length 340 mm; mean weight 301 g.

Condition factor = 1950-54, 0.63; 1956-61, 0.73; 1966-68, 0.77.

Fecundity increased as population size decreased.

32

Higley, D.L., and C.E. Bond. 1973. Ecology and production of juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, in a eutrophic reservoir. Fishery Bulletin 71:877-891.

Keywords: CHINOOK SALMON, NORTHWEST, ROTENONE, PREDATION, SUMMERKILL, INTRODUCTION, GROWTH, CONDITION FACTOR, COMPETITION

Abstract: Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, were reared in a central Oregon reservoir of 7.5 hectare. In 1961, epilimnion conditions of high pH, high temperatures, decreasing oxygen concentrations, and possibly algal toxins caused condition loss and deaths among salmon. Fry planted in 1961 (75,300) and in 1962 (150,000) suffered first-summer mortalities in excess of 80%, primarily due to predation by older salmon. Summer growth was rapid, but dependent on population densities. Coho salmon, *O. kisutch*, and chinook salmon remaining from a 1959 plant averaged 280 and 215 g after 30 mo. The 1961 year class averaged 62 g at 10 mo and 89 g at 22 mo. The 1962 year class averaged 22 g at 9 mo. Average condition factor values rose above 1.20 in the summer. Net production by the 1961 year class was 159 kg/hectare in 1961 and 35.5 kg/hectare in 1962. The 1962 year class produced 170 kg/hectare in 1962. Apparently competition from the 1962 year class caused the 1961 year class to feed more on littoral and terrestrial forms and to grow and produce less in their second year.

Data and Review: Higley and Bond studied the growth of chinook salmon fry introduced to a eutrophic reservoir in Oregon that had been treated with rotenone in 1960 to remove all salmonids. Fry were introduced in Feb., 1961 and March, 1962.

1961: 75,300 fry at 3,300/kg

1962: 150,000 fry at 2,200/kg

Density-dependent growth was observed for all year classes introduced. Salmon introduced in Jan., 1959 had reached average weights of 32 g (chinook) and 41 g (coho) when the lake was rotenoned in June, 1960. Surviving salmon reached 215 g (chinook) and 289 g (coho) by August 1961. The growth rate of the 1961 year-class was over twice that of the 1962 year-class. The remainder of the paper does not deal with compensation.

33

Cushing, D.H. 1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 5:847-854.

Keywords: MARINE, DENSITY-DEPENDENT GROWTH, LARVAE

Abstract: Haddock food-searching ability, size, mortality, feeding rates, densities, growth, and prey densities are used to determine whether haddock larvae can inflict significant mortalities on their prey. For the first 35 days after hatching, including the transition to exogenous feeding, haddock larvae must rely on a patchy food distribution as they need greater than average food densities. Afterward, increasing volume searched and food requirements may permit them to inflict significant mortalities on food organisms.

Review: The only data given are for haddock, except for some supporting evidence concerning mortality of herring and plaice. No data on compensation, but depletion of prey at early juvenile stage would be related to density-dependent growth. Useful for concepts of larval growth and feeding.

34

Crunkilton, R.L., J.M. Czarnecki, and L. Trial. 1980. Severe gas bubble disease in a warmwater fishery in the midwestern United States. Trans. Amer. Fish. Soc. 109:725-733.

Keywords: GIZZARD SHAD, WHITE BASS, FRESHWATER DRUM, GAS BUBBLE DISEASE, MIDWEST

Abstract: Gas bubble disease below Harry S. Truman Dam, sited on the upper Osage River and spilling into Lake of the Ozarks, caused the largest fish kill on record in Missouri. This is the first recorded evidence of serious supersaturation in the Midwest. Total gas saturation levels up to 139% killed nearly a half million fish in the upper 85 km of the Osage Arm, Lake of the Ozarks, during April-June, 1978 and 1979. Pelagic and near-shore species suffered the earliest and heaviest mortalities, but fish characteristic of deeper waters were increasingly killed as supersaturation persisted.

Data and Review: Major fish kills in Lake of the Ozarks below Harry S. Truman Dam in April-June 1978 and 1979 due to gas bubble disease are documented in this paper. The paper only reports data on gas saturation levels in the lake, mortality, and incidence of gas bubble disease in live fish. No information on the affected fish populations after the fish kills is presented; consequently, the paper is not valuable regarding compensation, but a follow-up study (if one has been published) would be very useful - especially regarding responses to catastrophic population reductions.

35

Bury, R.B. 1972. The effects of diesel fuel on a stream fauna. Calif. Fish and Game 58:291-295.

Keywords: RAINBOW TROUT, TOXIC, WEST

Abstract: The spillage of approximately 7,600 liters of diesel fuel into Hayfork Creek, California, resulted in a large kill of invertebrates, fishes, and other life. Over 2,500 fishes were killed, including lamprey ammocoetes (*Entosphenus tridentatus*), small-scaled suckers (*Catostomus rimiculus*), speckled dace (*Rhinichthys osculus*), and rainbow trout (*Salmo gairdneri*).

Data and Review: Similar to Crunkilton et al. (1980), in that this study only documents the catastrophic reduction of various vertebrate and invertebrate populations in a stream reach due to spillage of diesel fuel into the stream. The author indicated that several years of pre-spillage data are available, so that there is good potential for a strong follow-up study that would have valuable information on compensation.

36

Boaze, J.L., and R.T. Lackey. 1974. Age, growth, and utilization of landlocked alewives in Claytor Lake Virginia. Prog. Fish-Cult. 36:163-164.

Keywords: ALEWIFE, SOUTHEAST, INTRODUCTION, GROWTH

Abstract: Alewives were sampled from Claytor Lake, Virginia, an oligotrophic reservoir, in 1971 after 110,000 alewives had been introduced in 1968 and 1969 to increase forage in the lake. Fish sampled were analyzed for age and growth. The observed length-weight relation was $\log_{10} W = -5.28911 + 3.06370 \log_{10} L$. Age-1 fish collected in June 1971 were mature and age 0 fish were collected later that year, indicating successful reproduction. Rapid alewife growth appeared to be due to the existence of a vacant niche in the lake and abundant food resources.

Data and Review: Mean lengths of alewives were 81 mm at age 0, 154 mm at age 1, 187 mm at age 2, and 225 mm at age 3. These were large compared to other sites. This is a short paper; not much information is given.

Holden, A.V. 1973. Effects of pesticides on fish. Pages 213-253 in: Environmental pollution by pesticides. Plenum Press, New York, New York.

Keywords: REVIEW, BROOK TROUT, BLUEGILL, TOXICS, GROWTH

Abstract and Review: This paper is a review of literature on pesticide effects on fish. The section on growth in response to chronic toxicity is of interest concerning compensation. Holden found that compensatory growth (increased growth rate) occurred only when pesticides caused mortality in a "significant proportion" of the population. In studies where mortality rate did not increase, the growth rate did not change (relative to control populations). These results are not unexpected based on population regulation theory. In only one study (Crandall and Goodnight 1962 cited in this paper) did growth rate decline in population chronically exposed to a pesticide.

Bohnsack, J.A. 1983. Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. Environ. Biol. Fishes 9:41-53.

Keywords: ATLANTIC, "WINTERKILL", COMPETITION, PREDATION

Abstract: In January 1977, a record breaking cold spell caused fish kills at Big Pine Key, Florida. Census data collected before and after the cold spell from a series of model reefs constructed in 1975 showed a significant drop in mean number of reef fish species and individuals. Following this disturbance, high recruitment of juveniles occurred, presumably due to reduced competition, predation, or a combination of these. Model and natural patch reef communities examined the summer following the cold spell (1977) were significantly different from those examined the summer before (1976) and the second summer following the cold spell (1978). During the summer of 1977, a significantly smaller mean fish size and a significantly greater mean number of species and individuals were observed. Increased species richness following the cold spell is consistent with the intermediate disturbance hypothesis. Contrary to some theoretical predictions, results suggest reef fish communities are highly resilient to some regional disturbance.

Data and Review: A severe cold spell in January 1977 caused significant reduction in population sizes of resident reef fishes on experimental reefs in the Florida Keys. Populations remained low until summer 1977 when juvenile recruitment was very successful, apparently due to reduced mortality as a result of reduced competition and predation on the reefs. As a result, populations were greater in late 1977 than before the cold spell; however, population size returned to 1976 levels by mid-1978. It is difficult to tell from these data how much of the juvenile recruitment in 1977 resulted from immigration.

Chevalier, J.R. 1977. Changes in walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance, 1924-75. J. Fish. Res. Board Can. 34:1696-1702.

Keywords: WALLEYE, CANADA, OVERFISHING, DEWATERING, GROWTH, AGE AT MATURITY

Abstract: Annual commercial harvests of walleye (*Stizostedion vitreum vitreum*) from Rainy Lake steadily declined from 150,000 kg in the 1920s to 19,000 in the early 1970s. The walleye catch per unit of effort from commercial 102 mm gill nets declined from 43.63 kg/km in 1948 to 18.43 in 1969. Growth rate of walleye increased during 1959 to 1965, probably as a compensatory response to decreased abundance. The increased growth rate, in conjunction with heavy exploitation, caused the mean age of the walleye commercial catch to decline during 1957 to 1967. Both spring water levels and brood stock abundance were significant factors in walleye abundance 5 years later.

Data and Review: Records of annual commercial harvest of walleye from 1924 to 1975 in Rainy Lake, a large mesotrophic lake in the Boundary Waters region, were analyzed. Mean total length of age-4 walleye (back-calculated from age 4+ to 4) increased significantly between 1959 (37.34 cm) and 1965 (41.60 cm). Concurrently, population size (measured as catch per unit effort) declined from approximately 32 kg/km/day to approximately 20 kg/km/day (see Fig. 7); therefore increase in total length of age-4 fish likely reflects compensatory increase in growth rate in response to reduced population density. Mean ages of walleye in commercial catches declined significantly between 1955 and 1967 in both major sections of the lake (North Arm: 5.3 in 1957, 3.6 in 1967; East Arm: 6.5 in 1955, 4.4 in 1967). Because of increased growth rate, fish were becoming vulnerable to 102-mm gill nets at earlier ages and consequently decreasing mean age of catch. The author suggested that, since catch per unit effort did not increase over this time period, catch comprised of younger fish probably indicated that older age-groups were being lost from the population. No information is given on age at maturity or age-specific fecundity. Two factors were identified that appear to influence walleye abundance:

- 1) availability of spawning habitat as influenced by spring water level in the lake;
- 2) abundance of brood stock

Both spring water level and brood stock abundance at time t (years) are positively correlated with population size at time $t + 5$; only brood stock abundance was directly influenced by exploitation. However, lake water levels were largely controlled by a dam on the outlet from the lake (Rainy River) and, therefore, water level management practices could be partially responsible for the walleye population decline. At the present, the compensatory mechanisms that appear to be operating (increased growth rate, perhaps decreased age at maturity) are insufficient to maintain constant recruitment to the population.

Bagenal, T.B. 1977. Effects of fisheries on Eurasian perch (*Perca fluviatilis*) in Windermere. J. Fish. Res. Board Can. 34:1764-1768.

Keywords: EURASIAN PERCH, NORTHERN PIKE, BRITAIN, OVERFISHING, PREDATION, GROWTH, RECRUITMENT

Abstract: A review of literature indicated that a wartime (1941-48) trap fishery reduced the Eurasian perch (*Perca fluviatilis*) population considerably. An experimental gill net fishery for northern pike (*Esox lucius*) from 1944 to 1975 presumably contributed to keeping the perch population low through increased predation. The gill net fishery reduced the average size of the pike, and their growth rate increased, in turn increasing the predation on younger perch. This predation controlled recruitment to the adult perch population. Pike predation is given as one factor in a model explaining year-class fluctuations.

Data and Review: This paper is a review of the effects of perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) fisheries in Lake Windermere on perch populations in the two major basins of the lake (North and South). Perch were intensively fished during the war (1941-1947). Large scale removal continued until 1948 in the north basin and 1964 in the south basin; after that, only trap nets were set for sampling. Pike (the major predator on perch in the lake) have been gillnetted since 1944; the nets take fish >55 cm. Perch populations (abundance and biomass) were greatly reduced in both basins due to the wartime fishery (2 to 18-yr-old fish).

North: 58 metric tons in 1941, 10 metric tons in 1949

South: 80 metric tons in 1941, approximately 32 metric tons in 1949

There were concomitant changes in perch growth rate and sex ratio, but these changes are not well documented in this paper [see LeCren. 1958. J. Anim. Ecol. 27:287-331]. Perch populations increased in both basins in the mid- to late 1950s and reached peak biomass levels in 1961 and 1962 that exceeded 1941 biomass; populations steadily declined after 1962. Pike abundance increased from about 1,500 fish in 1945 to around 4,000 in 1969. Pike biomass remained relatively constant at around 3 metric tons from 1944 to 1969. Constant pike abundance (in terms of biomass) was due to changes in age distribution and growth rate. Pike were dominated by the 5-9 yr age-group in 1945. By 1975, dominance had shifted to fish <5 yrs old. Fish >9 yrs comprised about 10% of the population in 1945 but only <1% in 1975. Growth rates of pike in all age-groups increased between 1945 and 1975. For example, mean weights (kg) of age 7 fish were:

1944-45	males = 2.79	females = 5.73
1952-55	males = 2.95	females = 5.99
1972-75	males = 3.20	females = 7.26

Increases in mean weight were greatest for younger fish. Compensation (in terms of population biomass), caused by pike selectively removing older fish, occurred through increased numbers of younger fish and increased growth rates in all age-groups. Factors responsible for the increase in numbers of younger fish were not discussed. The increase in pike numbers was apparently sufficient to maintain the perch population at low levels due to the increased predation rate by pike on perch.

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Raleigh, R.F., D.H. Bennett, L.O. Mohn, and O.E. Maughan. 1978. Changes in fish stocks after major fish kills in the Clinch River near St. Paul, Virginia. Amer. Midl. Nat. 99:1-9.

Keywords: GIZZARD SHAD, SUCKERS, MINNOWS, SOUTHEAST, TOXIC SPILL

Abstract: Fish populations were sampled during 1973 and 1974 in a section of the Clinch River, near St. Paul, Virginia, that was subjected to chemically induced fish kills in 1967 and 1970. Species composition and relative abundance were compared with those from prekill, postkill and postkill recovery periods. A slight decrease in number of species and a change in relative abundance were found. Our data support the findings of others that general recovery following fish kills is relatively rapid.

Data and Review: Chemically-induced fish kills occurred in the Clinch River in 1967 and 1970. The 1967 kill reduced fish species richness from 15 species (plus two species groups - minnows and darters) to seven species (plus minnows). Fish abundance was reduced by 79% and virtually all benthic invertebrates were eliminated for the first 5-7 km below the chemical spill and greatly reduced for the next 120 km. The stream was restocked in 1968 with channel catfish, muskellunge, redbreast sunfish (*Lepomis auritus*), rock bass, smallmouth bass (*Micropterus dolomieu*), and walleye. Muskellunge and redbreast sunfish were not present or were very rare in the stream prior to the 1967 kill. The 1970 kill was less severe, killing 5,300 fish, but effects on species composition were not documented. The river and several tributaries were extensively sampled by electroshocking between 1973 and 1974. The major findings were:

- 1) There were 47 species collected postkill, 25 of which were minnows and darters (1973-1974), and 15 species (aside from minnows and darters) collected prekill (1964-1965). The differences could largely be attributed to the restocking program and to differences in collecting techniques and efficiencies between pre- and postkill sampling. Eleven species in the 1973-1974 sampling were represented by only one individual. Therefore, species richness was probably similar in pre- and postkill periods.
- 2) Relative abundances of species showed major shifts between pre- and postkill periods. Golden redbreast (*Moxostoma erythrum*) and gizzard shad were the most abundant species in prekill samples. Postkill

samples were dominated by shorthead redhorse (*M. macrolepidotum*), golden redhorse, carp, minnows (collectively), and northern hog sucker (*Hypentelium nigricans*).

- 3) Colonization of defaunated areas appeared to largely come from the river proper rather than from the nearest tributary. However, 30 of the 57 species present in 1973-1974 could have re-invaded from tributaries.

This study effectively showed that, in streams, immigration is a powerful means of recovering from catastrophic reductions in abundance. Without additional follow-up studies, it is difficult to interpret the shifts in community composition (i.e., relative abundances of species). It is possible that the 1973-1974 community had not yet reached an "equilibrium" and that, given sufficient time without disturbance, the community composition may return to prekill status.

42

Kenyon, R.B. 1978. Growth changes in a population of whitefish in Lake Erie. New York Fish and Game Journal 25:129-139.

Keywords: LAKE WHITEFISH, GREAT LAKES, OVERFISHING, GROWTH

Abstract: Experimental data collected from lake whitefish in the Pennsylvania waters of Lake Erie from 1971 to 1974 were used to describe the population since its drastic decline after the late 1940s. Growth was calculated and compared with that of the whitefish population of the late 1920s when the stocks were considered abundant. The lower rate of growth in recent years was deemed significant. A significant increase in weight per unit of length between the two periods was indicated by length-weight regressions (log transformations). Probable explanations for these changes are discussed, focusing primarily on climatology, the trophic state of Lake Erie and the zoogeography and abundance of whitefish.

Data and Review: Kenyon compared growth rates of Lake Erie lake whitefish (*Coregonus clupeaformis*) between 1927-1930 and 1971-1974. The 1927-1930 samples were taken while whitefish were still abundant in Lake Erie and they were heavily fished. The population declined markedly in the 1940s and was still very low during the 1971-1974 sampling. Growth rates were greater in 1927-1930 than in 1971-1974, largely due to slower growth of older age-groups in the 1970s. The author interpreted these differences as the result of compensation. He argued that growth rates were high in 1927-1930 because the population was responding to the fishing pressure. However, compensatory growth would also be expected in the 1970s because of the low population densities, but he contended that growth rates are low because of poor habitat quality. Consequently, it is difficult to make conclusions about compensatory growth by comparing the 1920s and 1970s populations because an additional variable, habitat quality, confounds the comparison.

Jensen, A.L. 1981. Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchill). J. Fish Biol. 19:557-573.

Keywords: LAKE WHITEFISH, GREAT LAKES, MODEL, AGE AT MATURITY, SURVIVAL, GROWTH, AGE-SPECIFIC FECUNDITY

Abstract: Mechanisms that might compensate for changes in mortality are well known but documentation of their operation and determination of their relative capacities is difficult. In this study the potential of lake whitefish to compensate for fishing mortality is quantified using a conventional fishery stock assessment model. The mechanisms examined are proportion of females, fecundity, survival of eggs and larvae, decrease in age at maturity, and growth. The change in each of these parameters necessary to maintain constant recruitment with increasing fishing pressure is determined. Decrease in age of maturity and increased survival of larvae and eggs have the greatest potential for compensation. The total capacity for compensation appears large even when the mechanisms are considered alone. A review of several lake whitefish population studies indicates a large variation in the vital statistics. There is a close relation between total mortality and growth. There is also a close relation between growth and age at maturity. The analyses indicate that increased fishing results in increased growth which then results in a lower age at maturity. This feedback mechanism enables lake whitefish to respond to changes in environmental conditions and on average to maintain a birth rate in balance with mortality.

Data and Review: Jensen applied the Beverton and Holt stock assessment model to lake whitefish populations to investigate which mechanisms might allow populations to maintain constant recruitment with increasing fishing pressure. Parameter estimates for the model were taken from studies of lake whitefish in northern Lake Michigan (see Jensen 1979 cited herein). Changes in sex ratio and fecundity were shown to have little potential to compensate for exploitation. Jensen reviewed data from several lake whitefish populations to determine which mechanisms appeared to be operating in nature. In all populations, exploitation was associated with faster growth and a decreased age at maturity. Model results showed that increase in growth rate alone cannot be an important compensatory mechanism; however, increased growth rate was related to other factors - increased fecundity and lower age at maturity. In the exploited populations, there was a significant relationship between growth rate and age at maturity (higher growth rate - lower age at maturity). Also there was a positive relationship between total mortality rate and growth rate. Jensen concluded that increased mortality (on mature individuals) reduced intraspecific competition, making more resources available per individual. This resulted in increased growth rate which in turn, resulted in decreased age at maturity and perhaps increased age-specific fecundity.

Jones, D.D., and C.J. Walters. 1976. Catastrophe theory and fisheries regulation. J. Fish. Res. Board Can. 33:2829-2833.

Keywords: MODELING, CATASTROPHE THEORY, OVERFISHING

Abstract: Catastrophe theory is a mathematical approach for analyzing systems that show abrupt changes. This paper attempts to apply the theory to fishery development and collapse, where the key variables are assumed to be stock size, level of economic investment or fleet size, and technological efficiency of the fishery gear. The analysis produces no new predictions about uncontrolled development and its consequences, but it appears to provide a useful way of exploring the implications of regulatory policies involving taxation, development subsidies, and technological improvement.

Review: This paper gives a clear statement of catastrophe theory, showing development of stock size - fleet size - fishing efficiency relationships and construction of a catastrophe manifold, a graphical 3-dimensional surface. The folded manifold is a "cusp catastrophe," where a small change in fleet size or efficiency results in stock collapse. This is applied to the Antarctic fin whale fishery. The paper states that Pacific salmon are another example, due to the advent of purse seining (increased efficiency), but no details are given. The authors suggested regulatory schemes based on the theory.

Walters, C.J., G. Steer, and G. Spangler. 1980. Responses of lake trout (*Salvelinus namaycush*) to harvesting, stocking, and lamprey reduction. Can. J. Fish. Aquat. Sci. 37:2133-2145.

Keywords: LAKE TROUT, GREAT LAKES, PREDATION, OVERFISHING, CATASTROPHE THEORY, AGE-SPECIFIC SURVIVAL, GROWTH, AGE AT MATURITY, MODELING.

Abstract: Sustained yields, declines, and recovery of lake trout (*Salvelinus namaycush*) can be explained by a simple model that hypothesizes normal population regulation through density dependent body growth, coupled with compensatory lamprey mortality. The model indicates that either lamprey or fishing alone could have caused the Lake Superior decline, though they apparently operated in concert. The presence of compensatory lamprey mortality leads to a "cliff edge" in the system's dynamics, such that catastrophic changes may be repeated in the future. It is not unlikely that Lake Superior is on the verge of a second collapse.

Review: The authors used data from many lake trout studies as parameters for a model demonstrating lake trout decline and recovery. Catastrophe theory is used to demonstrate large changes in stock biomass resulting from small changes in fishing effort and lamprey abundance when stock is too close to the "cliff edge". Many useful references are given. The authors related model to

policy. A good overview is given of lake trout population dynamics in Lakes Michigan and Superior, despite simplifications in the model (e.g. same reproductive success assumed for planted and native fish). Early warning indicators for lake trout are decrease in native yearling ratio, decrease in abundance of large fish, and increase in body weight of fish < age 8. Fishing and lamprey predation decrease the domain of stability of spawner biomass; i.e., upper equilibrium biomass moves closer to lower critical biomass.

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McFadden, J.T. 1977. An argument supporting the reality of compensation in fish populations and a plea to let them exercise it, p. 153-183. In W. Van Winkle [ed.] Proceedings of the conference on assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press Inc., New York. 380 p.

Keywords: REVIEW

Data and Review: An iconoclastic, eclectic review of the literature on compensation in fish populations. McFadden reviewed what is meant by compensation, gave a historical review of the development of the concept, and then argued for the widespread occurrence of compensation in fish populations based on a discussion of density-dependent and density-independent models of population growth and Ricker's stock-recruitment models. [Table 1 (pp. 169-170) gives 17 examples of compensation.] He concluded with a section dealing with the applicability of fisheries dynamics principles to power plant impacts. He argued (based on Ricker 1954) that the principles of fisheries management can be applied to power plant impacts (largely directed at early life history stages) and that "fish populations can readily sustain 'exploitation' by power plants at levels comparable to those experienced in commercial and sport fisheries."

47

Butler, R.L. 1965. Freshwater drum, (*Aplodinotus grunniens*), in the navigational impoundments of the upper Mississippi River. Trans. Amer. Fish. Soc. 94:339-349.

Keywords: FRESHWATER DRUM, MORTALITY RATES, YEAR-CLASS STRENGTH, MIDWEST

Abstract: Scale samples from fish taken during the years 1944 through 1948 were used to analyze the freshwater drum fishery of the Upper Mississippi. Total and fishing mortality rates were calculated for heavily and lightly fished populations in the impoundment system of 26 dams. Mortality rates of drum from the northern section of the river were compared with those from the southern section. Weak year classes were formed during 1942, 1943, and 1945, and strong year classes were formed during 1941 and 1944. Strength of year class was directly related to air and water temperature during May but not to water stage during the spawning season.

Data and Review: Fluctuations in drum year-class strength were related to air and water temperature. An argument was given that larva mortality rates are dependent on changes of temperature and thus ultimately determine year-class strength. However, no supporting data on larva mortality or their response to temperature were provided.

48

Swedburg, D.V., and C.H. Walburg. 1970. Spawning and early life history of the freshwater drum in Lewis and Clark Lake, Missouri River. Trans. Amer. Fish. Soc. 99:560-570.

Keywords: FRESHWATER DRUM, FECUNDITY, FEEDING, YEAR-CLASS STRENGTH, MIDWEST

Abstract: The early life history of freshwater drum, (*Aplodinotus grunniens*), was studied in 1965-1967 to determine factors influencing year-class strength in a main stem Missouri River reservoir. Fish spawning occurred over a period of 6-7 weeks in June and July when water temperatures reached 18°C. Fecundity of fish 307 to 386 mm long and 6-9 years old ranged from 34,000 to 66,500 ova. Ova reared in the laboratory at a water temperature of 23°C hatched in 27 h and the prolarvae averaged 3.2 mm long. The prolarval stage was complete 45 h after hatching and postlarvae averaged 4.4 mm long. Adult characters developed at an approximate length of 15 mm. Diet of fish 6-15 mm long was *Daphnia* and *Cyclops*. Bottom fauna became important in the diet of fish longer than 20 mm. Fish movement between channel and floodplain was related to changes in diet. Growth, year-class strength, and mortality varied among years. Strong year classes were associated with warm summer (June-August) water temperatures in the spawning and nursery area and weak year classes with cold temperatures. Size of year class was determined before fish attained a length of 25 mm.

Data and Review: Much of this paper provided background information on fecundity, larval development, larval and juvenile food, movement of larvae, and factors influencing year-class strength. A relationship was drawn between year-class strength of drum over three years and summer water temperatures (as cumulative degree days). Warm temperatures coincided with strong year-classes whereas cold temperatures coincided with weak year-classes. Mortality curves for age-0 fish indicated the differences in year class strength could not be accounted for by different mortality rates over the three years for fish between 25 and 94 mm long. The authors, therefore, argued that much of the mortality that determined year class strength must have been for fish less than 25 mm long. However, they were unable to actually measure such mortality and thus could not support this claim with actual data.

Priegel, G.R. 1971. Evaluation of intensive freshwater drum removal in Lake Winnebago, Wisconsin, 1955-1966. Tech. Bull. Number 47, Wisc. Dept. Nat. Res., Madison, Wisconsin. 29 p. Keywords: FRESHWATER DRUM, EXPERIMENTAL FISHING, CONDITION, RECRUITMENT, INTER- AND INTRASPECIFIC COMPETITION, MIDWEST

Abstract: An intensive freshwater drum removal program was undertaken on Lake Winnebago with assistance of qualified commercial fishermen in 1955. A 12-year evaluation study, 1955-1966, was initiated at the start of the intensive removal program to evaluate the effects of freshwater drum removal on the freshwater drum population and other species. From 1955 through 1966, 15 million kg of freshwater drum were removed from Lake Winnebago. Initial heavy removal, 5 million kg of freshwater drum in 1955-57, resulted in a decided change in the condition of freshwater drum; however, the improvement in condition that was evident early in the study tended to be lost later. The commercial harvest was intensive enough to crop off the larger and older freshwater drum by 1962 so that the harvest after 1962 was composed of smaller and younger fish even though rate of growth remained the same. Selected trap net sets during April-June and trawling during the summer and autumn were effective methods of removing freshwater drum. To keep the freshwater drum population at an optimum size in Lake Winnebago, 1.1-1.3 million kg should be removed annually. Since the freshwater drum is very prolific fish and occupies a favorable habitat, the population would soon consist of many slow-growing, old-age fish, which was the situation before the program began in 1955, if maximum effort is not maintained. There were benefits to the sport fishery that appeared to result from the freshwater drum removal program; however, no positive correlation could be demonstrated. There was no indication that commercial removal of freshwater drum was detrimental to any game or panfish population.

Data and Review: After intensive removal of freshwater drum over a 12 year period by commercial fishermen in Lake Winnebago, the change in the numbers or biomass of the population appeared to be negligible based on the catch-per-unit effort data provided. The author claimed, however, a substantial decline in the drum population occurred but based his conclusion upon total catch data which would be biased due to varying fishing intensity. As CPUE remained steady in both numbers and biomass, and age composition shifted to younger fish, recruitment must have improved, possibly due to decreased intraspecific competition. The condition factor of drum fluctuated over the study period with no consistent trend. Figures and text on condition factor in this paper do not agree, making it difficult to evaluate the author's interpretation. The suspicion here was that compensation must have occurred to maintain the drum population despite intensive removal of adults. However, the mechanism for this could not be ascertained based on the data presented. CPUE of white bass (*Morone chrysops*), black crappie, and sauger rose strikingly after drum removal. Sauger were most abundant in 1960 and 1964, dropping back down to pre-experiment levels in 1961-1962, whereas white bass and black crappie peaked in 1961-1962 and then dropped. This apparent inverse relationship, coupled with the changes in freshwater drum condition, suggests that some complex competitive community interactions were occurring.

Cada, G.F., and G.L. Hergenrader. 1980. Natural mortality rates of freshwater drum larvae in the Missouri River. Trans. Amer. Fish. Soc. 109:479-483.

Keywords: FRESHWATER DRUM, LARVA MORTALITY, MIDWEST

Abstract: Instantaneous total mortality rates for planktonic larval freshwater drums (*Aplodinotus grunniens*) in a channelized stretch of the Missouri River were estimated from analyses of cumulative catch curves. Mortality rates, which ranged from 0.11 to 0.21 per day, were significantly greater in 1976 than in 1974. Basing our interpretation on the underrepresentation of eggs and early larvae in the channelized river samples, we hypothesize that favorable environments upstream represent a more significant source of recruitment of larvae to the freshwater drum population than the channelized river.

Data and Review: A method was described to effectively assess larva mortality rates for a natural population of drum based of length-frequency data of larvae caught in plankton nets. Consideration was given to sampling inefficiency for some size groups of larvae, so mortality rates were estimated only for fish between 5 and 11 mm long. Results of sampling drum for two years on the Missouri River showed significant differences in mortality between years but not within a year for two separate sampling stations. No causes for the difference were given nor was the impact on year-class strength known. The lack of larvae less than 5 mm long was probably due to spawning and early development having taken place upstream and not in the sampling area considered. Thus, later larval stages taken in the samples were drifting downriver from these spawning areas. In rivers, compensation would be more difficult to detect due to extensive immigration from upstream.

Bardach, J.E. 1951. Changes in the yellow perch populations of Lake Mendota, Wisconsin, between 1916 and 1948. Ecology 32:719-728.

Keywords: YELLOW PERCH, MIDWEST, DISEASE, COMPETITION, GROWTH, CANNIBALISM

Abstract: Data from 1916-1948 on yellow perch from Lake Mendota, Wisconsin were collated and discussed. There was a general decrease in the number of yellow perch over the last 50 years and a concomitant increase in their size (doubled). The decline in abundance and growth improvement were related to disease (myxosporidian of the genus *Myxobolus*), reduction in the numbers of a competing species (lake herring), and an increase in fishing pressure. The disease also reduced cannibalism on younger perch because larger yellow perch were the most affected by the disease. The most noticeable acceleration in growth rate occurred in 1939 when the disease reached epizootic proportions. From 1916 to 1947 there was an approximate 4.3-fold decrease in catch/effort.

The average total length increased from 162 to 243 mm and mean weight went from 50 to 180 g or 3.6 times its former level. Condition factor improved from 1.18 in 1916 to 1.25 in 1948.

Data and Review: Bardach's paper generally supports some of the compensatory responses seen in other studies. All the conclusions are based on circumstantial evidence and co-occurring events and are not strongly supported, but believable.

52

Wells, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954-75. J. Fish. Res. Board Can. 34:1821-1829.

Keywords: YELLOW PERCH, LAKE MICHIGAN, ALEWIFE, COMPETITION, PREDATION, OVERFISHING

Abstract: In the early and mid-1960s yellow perch in Lake Michigan declined, which was related to the alewife invasion. An intensive commercial fishery hastened the decline. High production in the commercial fishery was related to increased growth of remaining perch (growth compensation).

Data and Review: This is a good discussion of the impact of an exotic species on yellow perch. The mechanism for the impact was speculated to be predation on yellow perch larvae by alewife. Catches of yellow perch over 1962-1975 are given. An excellent table (3) showing growth of perch is given. For example, female yellow perch of age 4 were 189 mm in pre-alewife days (1954), then after alewife appeared in the 1960s, age-4 yellow perch averaged 203 mm (1963), 222 mm (1964), 267 mm (1970) and 241 mm (1975).

53

Fraser, J.M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. Trans. Amer. Fish. Soc. 107:505-517.

Keywords: ONTARIO, YELLOW PERCH, COMPETITION, GROWTH, SURVIVAL

Abstract: Brook and rainbow trout and splake were stocked in a lake for 12 yr. Yellow perch were introduced after the first 6 yr. Mean return per kilogram of trout stocked decreased from 3.3-6.8 kg to 0.4-0.9 kg after perch were introduced. Yellow perch dominated the fish community (20-30 kg/ha) and caused a change in the food eaten by salmonids which resulted in a 50% decline in growth rates. Salmonids could not compete with the yellow perch.

Data and Review: This study is a classic example of competition between yellow perch and salmonids. Good data are given on biomass of yellow perch and of salmonids, before and after perch were stocked. Evidence of repression of the following year class of yellow perch by the 1969 year class, possibly due to

competition, is presented in Fig. 4. Some growth data are also presented. Yellow perch grew well to age 2, then barely grew at all. Members of the 1967 year class of yellow perch reached 240 mm in 26 mo, surpassing growth rates for most waters. Growth ceased after 240 mm. Yellow perch growth rate declined after they became established. The only negative interaction between species was believed to be competition for food, as salmonids did not eat any yellow perch or vice versa.

54

Grice, F. 1959. Elasticity of growth of yellow perch, chain pickerel, and largemouth bass in some reclaimed Massachusetts waters. Trans. Amer. Fish. Soc. 88:332-335.

Keywords: YELLOW PERCH, NORTHEAST, GROWTH, LARGEMOUTH BASS, COMPETITION, ROTENONE

Abstract: Massachusetts ponds and lakes were reclaimed with rotenone. Growth rates of several species, including yellow perch, increased after reclamation, probably due to reduced competition for food. Rate of growth was more dependent on density than length of growing season.

Data and Review: This is another good example of the response of yellow perch and several other species to decreased inter- and intraspecific competition, primarily for food. Growth in some of these lakes was as rapid as any previously observed, demonstrating the maximum capacity for growth for these species. Some excellent growth data are given in Table I on a wide range of lakes and ponds.

55

Kelso, J.R.M., and T.B. Bagenal. 1977. Percids in unperturbed ecosystems. J. Fish. Res. Board Can. 34:1959-1963.

Keywords: YELLOW PERCH, GROWTH, SURVIVAL, RECRUITMENT, REVIEW

Abstract: A review of yellow perch in unperturbed systems showed these areas to be harsh environments and rarely studied, with growth being low and variable. Temperature stands out as a major factor affecting yellow perch growth, but a general growth rate applicable to all unperturbed populations cannot be identified. Particular year classes dominated a population in lakes undergoing light to no exploitation, but domination by a year class was less marked in perturbed systems (e.g., Windermere). Unperturbed systems usually have a wide range of age-groups present. Survival ranges from 27 to 69%. Conservation of biomass was a consistent feature of yellow perch populations.

Data and Review: This is a literature review giving a good overview of unperturbed systems. Such systems are valued as good hypothesis testing opportunities. Growth, survival, and recruitment are compared between perturbed and unperturbed systems.

56

Nakashima, B.S., and W.C. Leggett. 1975. Yellow perch (*Perca flavescens*) biomass responses to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec-Vermont. J. Fish. Res. Board Can. 32:1785-1797.

Keywords: YELLOW PERCH, COMPETITION, GROWTH, MORTALITY, NORTHEAST

Abstract: Perch biomass in Lake Memphremagog, Quebec was 2.5 times greater in the more productive south than in the less productive north basin. A large perch population existed in the south basin; growth was similar in both basins. This study provided empirical support that with abundant food supply, population size and not growth is enhanced.

Data and Review: The data and conclusions from this study provide empirical verification of the compensation phenomenon, that when a fish is near maximum growth, its ability to compensate through growth is reduced. In this study, perch were growing at or near their maximum levels for Quebec; therefore, with increased eutrophication and an abundant supply of food, growth did not increase (as often is the case when perch are below maximum). Greater food supplies in the south basin increased survival of young perch. YOY perch were 5-10 times more abundant in the south than the north basin, while older perch were only about two times more abundant, so compensation occurred in the early life stages and tapered off later. Growth and mortality rates are given. Summer and fall predation played a small part in regulating YOY populations. Cannibalism rarely occurred. Rainbow smelt were the main forage fish of several species, including yellow perch.

57

Ryan, P.M., and H.H. Harvey. 1980. Responses of yellow perch, *Perca flavescens* (Mitchill), to lake acidification in the La Cloche mountain lakes of Ontario. Env. Biol. Fish. 5:97-108.

Keywords: YELLOW PERCH, CANADA, GROWTH, RECRUITMENT, INTRASPECIFIC COMPETITION, SURVIVAL, ACIDIFICATION

Abstract: Yellow perch in acidified lakes of Ontario had reduced densities. Perch of age-group 1-3 responded with increased growth, while those aged 4-9 had decreased growth. Thus, growth rate was proposed as an indicator of environmental stress.

Data and Review: This paper presents growth data on 1,667 yellow perch from 38 Ontario lakes subject to acidification and offers the premise that perch growth rates, which are subject to complicating density-dependent factors such as predation and competition, can act as indicators of water quality and environmental stress. Extensive data are given on all lakes for yellow perch growth each year. Mean length of yellow perch at a given age vs. lake pH relationships indicated that growth changes were occurring in an accelerating manner with decreasing lake pH. The more acid the lakes the less successful was recruitment. These results support the hypothesis that the mechanism of increased growth rate of the younger age-groups at high acid levels was through lowered population densities due to recruitment or reproductive failure. Improvements in growth of the younger age-groups can be attributed to increases in the available food supply per individual as mortality rates increased. These losses may have diminished interspecific or intraspecific competition. Perch were among the most acid tolerant of 30 species investigated. Thus young perch in lakes in the 4.5-5.5 pH range may experience greatly reduced competition for invertebrate food, reduced population density, failure of recruitment of year classes, elimination of acid-sensitive individuals from populations and random loss via episodic acid events in spring. Increased maintenance requirements for older fish cause mortality and, if mortality increases beyond a certain point, reduced recruitment and sometimes population extinction.

58

Tarby, M.J. 1974. Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. Trans. Amer. Fish. Soc. 103:462-471.

Keywords: YELLOW PERCH, CANNIBALISM, NORTHEAST, YOY SURVIVAL, PREDATION

Abstract: Yellow perch in Oneida Lake, New York, were studied from 1965 to 1971 to identify the factors affecting the intensity of cannibalism and to evaluate the effect of cannibalism on the abundance of young perch. Wide variations occurred in the annual intensity of cannibalism. Cannibalism was most intense in August and operated as a density-independent factor. Walleye predation on yellow perch YOY caused compensatory mortality of young perch, implying that cannibalism was not decisive in limiting the strength of year classes in 1965-71 in Oneida Lake.

Data and Review: This is a very good paper with well documented data on cannibalism. Tarby used multiple regression analysis to identify length and abundance of young perch as the most important factors controlling the intensity of cannibalism. The positive relationship between the incidence of perch cannibalism and the abundance of young suggested that cannibalism operates as a compensatory mortality factor. Tarby believed intuitively that high densities of YOY yellow perch should operate as a density-dependent compensatory factor and cause decreased growth in August; however, growth remained unchanged over the period of most intense cannibalism. This implied that cannibalism was density-independent and unrelated to young perch abundance. Forney (1971) attributed most mortality of young perch during the

demersal stage to walleye predation. Total mortality of yellow perch from August to the following May generally exceeded 96%; cannibalism (mostly during August) was a very small component of this total mortality. By the time cannibalism peaked, walleyes had already consumed two-thirds of the perch year class, reducing the potential impact of cannibalism on the abundance of young perch. Cannibalism by yellow perch along with walleye predation can in certain years suppress yellow perch YOY abundance.

59

Deelder, C.L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. Hydrobiologia 3:357-378.

Keywords: YELLOW PERCH, EUROPE, GROWTH, STARVATION

Abstract: Studies of stunting of yellow perch in Holland were conducted to determine why it occurred. Deelder found that perch reached about 13 cm then hardly grew, and attributed this to lack of food for these large fish which starved to death. This confirmed observations of other authors. Although suitable prey existed in these waters, extensive plant beds provided refuges for prey and prevented perch from successful feeding.

Data and Review: This is an interesting discussion of anomalous growth in perch. It speaks to the importance of suitable, available food for the continued good growth of perch.

60

Craig, J.F., C. Kipling, E.D. LeCren, and J.C. McCormack. 1979. Estimates of the numbers, biomass, and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1967 to 1977 and some comparisons with earlier years. J. Anim. Ecol. 48:315-325.

Keywords: YELLOW PERCH, ENGLAND, LAKE WINDERMERE, DISEASE, COMPETITION

Abstract: Estimates of the numbers, biomass (to 1977), and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere are given. Wire-netting traps were used to remove and collect yellow perch; catch per unit effort varied widely throughout the study period, 1961-1977. Mortality rates are given for male perch from 1955 to 1972. Numbers of age-2+ perch were high in 1941, fell rapidly, and then continued to decline until 1950. Strong year classes in 1955 and 1959 increased the numbers in the lake rapidly. Poor recruitment after 1959 resulted in a decrease in numbers. Despite the fact that numbers of perch in the lake in 1941 were considerably higher than those from 1967 to 1976, the biomass values were very similar. This was the result of a change in growth, showing that the population tends toward stability of biomass, not numbers. A disease in 1976 killed 98% of the adult perch in the lake. Catches went from 6,000 in May-June 1976 to 128 in 1977.

Data and Review: This is a good paper but more follow-up on the yellow perch die-off would have been preferred, a common problem with many of these types of studies. However this study presents many data on mortality rates, abundance, changes in the population when the disease struck, and information on year-class strength. Some data are also given on abundance of the various age-groups of fish. Craig (1980) mentioned that age at maturity decreased to 2 years following the 1976 epidemic, while perch had matured at age 3+ before the disease.

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Clady, M.D. 1976. Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. J. Fish. Res. Board Can. 33:1887-1893.

Keywords: YELLOW PERCH, NORTHEAST, LARVAL AND EGG SURVIVAL, STRESS, DENSITY-INDEPENDENT FACTORS

Abstract: Survival from the egg to larval stage was estimated for the 1969-1975 year classes of yellow perch in Oneida Lake. Egg production and abundance of larval fish were determined. Early survival varied from 1.6 to 18.4% and was correlated positively with temperature and negatively with wind. Physical destruction and movement of eggs by high winds and greater mortality of prolarvae because of low temperature could account for the differences in survival between years, but were not severe enough to wholly account for the >80% mortality which occurred in each year. The low year-to-year variation in survival suggests that temperature and wind influenced year-class size through a complex of many relatively minor mortality factors, rather than through one catastrophic event.

Data and Review: Data are given on the number of mature yellow perch in Oneida Lake from 1969 to 1975 as well as estimates of fecundity, number of larvae produced, and survival to the 8-mm stage. The multi-age character of the adult stock and the low and constant mortality experienced by adult perch contributed to stability in the number of eggs produced each year. The multi-stock character of perch minimized the effect of differences in numerical size of year classes. Mortality of prolarvae was presumed to be low. Clady's important conclusion was that many relatively small mortality factors combined to produce the high mortality eventually experienced by YOY yellow perch.

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Eshenroder, R.L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34:1830-1838.

Keywords: YELLOW PERCH, GREAT LAKES, OVERFISHING, GROWTH, COMPETITION, ALEWIFE, RAINBOW SMELT, WALLEYE

Abstract: The yellow perch population in Saginaw Bay is discussed with regard to historical changes and more recent (1960-1970s) fluctuations. Intensified effort and size limit removal resulted in exceptional landings of yellow perch from Saginaw Bay. Effort concentrated in the outer bay, then shifted to the inner bay. Yellow perch growth rate increased, and older age-groups were no longer prominent in the catches. Females became relatively scarce shortly after attaining vulnerability to fishing gear. The low recruitment of the late 1960s and early 1970s may have been related to reduced brood stocks. In the 1940s yellow perch were most affected by loss of the walleye; predation by walleye apparently held down yellow perch populations, resulting in good perch growth. When the walleye population collapsed in the 1940s, yellow perch abundance increased and growth slowed. Rainbow smelt and alewife affected perch by competition and predation in the 1950s, but overfishing had the most intense effect in the 1960s-1970s. Spring temperature had an important role in reproductive success of yellow perch.

Data and Review: This is a very good discussion of the behavior of yellow perch stocks in Saginaw Bay. Commercial fishing effort and landings are given from 1880 to 1976, demonstrating how the fishery affected perch stocks after removal of the size limit. Older fish were removed from the population, females more than males; growth increased, and recruitment was lowered. Eshenroder presented a table of growth data covering 1929 to 1970 by year of life, plus data on percentage of fish in each age-group. Temperature and year-class strength showed a strong positive relationship.

APPENDIX 2

Author-Date List of Literature Checked for Information on Compensation

Numbers at ends of lines refer to order of placement in Annotated Bibliography, Appendix 1

Key to Codes

X = no copy made; no information on compensation or catastrophe
C = contains information on compensation; N = no information on compensation
S = catastrophic event occurred; N = no catastrophic event
Y = contains data for quantifying compensation; N = no data
R = reviewed; N = not reviewed

Adams, J. R.	1969	
Agersborg, H. P. K.	1930	NCNN
Ahlstrom, E. H.	1966	X
Albaugh, D. W.	1969	
Alcorn, D. J., L. E. Fancher, and J. G. Moss	1980	NNNR 24
Alderdice, D. F. and J. R. Brett	1957	X
Alexander, D. R. and H. R. MacCrimmon	1974	X
Allen, K. R.	1935	
Allen, K. R.	1938	
Alm, G.	1952	
Alsop, R. G. and J. L. Forney	1962	
Anderson, E. D. and L. L. Smith	1971	
Andrews, A. K., C. C. Van Valin and B. E. Stebbings	1966	CSYR 31
Anonymous	1966	
Anthony, D. D. and C. R. Jorgensen	1977	
Armstrong, G. C.	1949	X
Ash, G. R., N. R. Chymko and D. N. Gallup	1974	X
Atton, F. M.	1959	X
Austin, H. M., A. D. Sosnow and C. R. Hickey Jr.	1975	
Avault, J. W. Jr., C. L. Birdsong, and W. G. Perry Jr.	1969	X
Bagenal, T. B.	1970	
Bagenal, T. B.	1977	CSYR 40
Bagenal, T. (ed.)	1978	X
Bagenal, T. B.	1982	
Bailey, M. M.	1964	
Bailey, W. M.	1978	
Baldwin, N. S.	1968	X
Ball, R. C.	1945b	
Ball, R. C.	1945a	
Balon, E. K.	1983	
Bardach, J. E.	1951	CNYR 51
Barica, Jan	1975	X
Barica, Jan	1977	X
Barica, Jan and John A. Mathias	1979	X
Barnthouse, L. W., J. Boreman, S. W. Christensen and others	1984	
Barton, Bruce A.	1977	X
Beamish, R. J. and H. H. Harvey	1972	NSNR 26
Beamish, R. J.	1976	
Beckman, William C.	1941	CSYR 1
Beckman, William C.	1943	CSYR 2
Beckman, William C.	1950	CSYR 3
Beddington, J. R. and R. M. May	1977	X
Beers, G. D. and W. J. McConnell	1966	
Beeton, A. M. and W. T. Edmondson	1972	
Beiningen, K. T. and W. J. Ebel	1970	X
Beland, R. D.	1953	X
Bellamy, D. J., P. H. Clark, D. M. John, D. Jones and others	1967	X
Bell, G. P., P. Handford and C. Dietz	1977	
Bella, David A. and K. J. Williamson	1979	X
Bender, E. A., T. J. Case, and M. E. Gilpin	1984	
Bennett, George W.	1945	
Bennett, George W.	1954	

Bennett, George W.	1970	
Bennett, George W., H. Wickliffe Adkins and William F. Childers	1973	
Benson, N. G.	1973 X	
Bergstedt, R. R. and R. O'Gorman	1983	CSYN
Berst, A. H. and A. A. Wainio	1967	
Berst, A. H. and G. R. Spangler	1972	
Berst, A. H. and G. R. Spangler	1973	
Bergstedt, R. R. and R. O'Gorman	1983	
Beverton, R. J. H. and S. H. Holt	1957 X	CSNR
Beverton, R. J. H.	1962	
Beyerle, G. B. and E. L. Cooper	1960	
Bidgood, B. F.	1973	
Bigelow, H. B. and W. C. Schroeder	1953	
Birch, L. C.	1957 X	
Bishop, Keith A.	1980 X	
Blaber, S. J. M. and A. K. Whitfield	1976 X	
Blockman, R. A. A. and R. J. Low	1981 X	
Blumer, Max, H. L. Sanders, J. F. Grassle, and G. R. Hampson	1971	
Boaze, John L. and Robert T. Lackey	1974	NNYR 36
Bodola, A.	1966	NNYN
Bohnsack, J. A.	1983	NSNR 38
Borawa, James C., J. H. Kerby, M. T. Huish, and A. W. Mullis	1978	
Boreman, J.	1974 X	
Bouck, G. R.	1980 X	
Bowers, C. C.	1955 X	
Brander, K.	1981 X	
Brazo, D. C., P. I. Tack, and C. R. Liston	1975	
Bregazzi, P. R., and C. R. Kennedy	1982 X	NNNN
Brewer, G. D.	1978	
Brooker, M. P., D. L. Morris and R. J. Hemsworth	1977 X	
Brown, M. E.	1946	
Brown, E. H., Jr.	1968	CSYN
Brown, Edward H., Jr.	1972	CSYN
Brownell, C. L.	1984	CNNN
Brungs, William A.	1973 X	
Brussard, P. F., M. C. Hall, and J. Wright	1981 X	NNNN
Bryant, H. E. and A. Houser	1968	
Brynildson and Kempinger	1973	
Brynildson, O. M. and J. J. Kempinger	1973	
Buck, D. H. and C. F. Thoits III	1970	
Budd, J. C. and D. Cucin	1962 X	
Bulkley, Ross V.	1970	
Bullock, L. H. and G. B. Smith	1979 X	
Burbidge, R. G.	1969	
Burnet, A. M. R.	1959	
Burns, J.	1966b	
Burns, J.	1966aX	
Burns, Kathryn A. and J. M. Teal	1979 X	
Burrough, R. J., P. R. Bregazzi, and C. R. Kennedy	1979	CNNR 14
Burrough, R. J. and C. R. Kennedy	1979	CSYR 13
Bury, R. B.	1972	NSNR 25
Busch, Wolf-Dieter N., R. L. Scholl, and W. L. Hartman	1975	

Busch, W. D. N., D. H. Davies, and S. J. Nepszy.....	1977	
Butler, R. L. and L. L. Smith Jr.....	1949	
Butler, R. L.....	1965	NNR 47
Butler, James N. and E. M. Levy.....	1978 X	
Cada, G. F. and G. L. Hergenrader.....	1980	NNR 50
Calhoun, A. ed.....	1966	
Calow, P.....	1973	
Cambray, J. A.....	1983	
Campbell, R. N.....	1971	
Canter, L. W. and L. G. Hill.....	1979 X	
Carlander, K. D.....	1945	
Carlander, K. D.....	1945b	
Carlander, K. D.....	1945a	
Carlander, K. D.....	1950 X	
Carlander, K. D. and R. R. Whitney.....	1961 X	
Carlander, K. D.....	1977	
Carlander, K. D. and P. M. Payne.....	1977 X	
Catt, J. and A. W. H. Needler.....	1946	
Chan, John G. and Stephen-Hassard, Q. D.....	1977 X	
Chapman, D. W.....	1962	
Chapman, D. W.....	1966	
Chapman, D. W.....	1967	
Chapman, D. W. and E. Knudsen.....	1980	
Chavin, W.....	1964 X	
Chevalier, J. R.....	1973	
Chevalier, J. R.....	1977	CNVR 39
Christie, W. J.....	1968	
Christie, W. H.....	1972	
Christie, W. H., J. M. Fraser, and S. J. Nepszy.....	1972	
Christie, W. J.....	1973	
Christie, W. J.....	1974	
Christie, W. J.....	1976	
Churchill, Warren.....	1957	
Clady, M. D.....	1967	
Clady, M. and B Hutchinson.....	1975 X	
Clady, M. D.....	1976	
Clark, F. N. and J. B. Phillips.....	1952	NNR 61
Clark, C. W.....	1973 X	
Clark, C.....	1974	
Clark, Robert C. Jr., B. G. Patten, and E. E. De Nike.....	1978 X	
Clavin, W.....	1964 X	
Clemens, Howard P. and M. Martin.....	1952	
Clepper, H. ed.....	1979	
Clugston, James P., D. Hugh Barwick, and T. T. Fendley.....	1982	
Coble, Daniel W.....	1971 X	
Cohen, E. B., G. C. Laurence and W. G. Smith.....	1984	
Coker, Coit M. and E. H. Hollis.....	1950 X	
Colby, P. J. and L. T. Brooke.....	1968 X	
Colby, Peter J.....	1971 X	
Colby, P. J., G. R. Spangler, D. A. Hurley, A. M. Mc Combie.....	1972	
Colby, P. J.....	1973	
Cole, L. C.....	1951	

Cole, L. C.	1954	
Collins, R. A.	1971	
Collette, B. B., M. A. Ali, K. E. F. Hokanson and others	1977 X	
Combs, D. L.	1980	---N
Connell, Cecil H. and J. B. Cross	1950 X	
Cooper, E. L.	1953	
Cooper, E. L.	1967.	
Cope, O. B., J. P. McCraren and L. Eller	1969	
Copeland, B. J.	1970 X	
Cope, O. B., E. M. Wood, and G. H. Wallen	1970	
Cordone, A. J. and S. J. Nicola	1970 X	
Cox and Contant	1976	
Craig, J. F., C. Kipling, E. D. Le Cren, and J. C. McCormack	1979	CNYR 60
Craig, J. F.	1980	CSYN
Crance, Johnnie H.	1965 X	
Crance, J. H. and L. G. McBay	1966	
Crecco, Victor A. and Mark M. Blake	1983	
Crecco, V. A. and T. F. Savoy	1984	NNNN
Cretney, W. J., C. S. Wong, D. R. Green and C. A. Bawden	1978	
Crowder, Larry B.	1980	
Crunkilton, R. L., J. M. Czarnecki, and L. Trial	1980	NSNR 34
Cucin, D. and H. A. Regier	1966	
Cushing, D. H.	1974	
Cushing, D. H.	1975	
Cushing, D. H.	1983	NNNR 33
Dahl, F. H. and R. B. McDonald	1980 X	NNNN
Daiber, F. C.	1952 X	
Daiber, F. C.	1953	
Davidoff, E. B., R. W. Rybicki, and K. H. Doan	1973	
Davies, R. M., and coauthors	1976	
Davies, J. M., R. Hardy and A. D. Mc Intyre	1981 X	
De Mont, D. J. and R. W. Miller	1971 X	
Deason, H. J.	1933 X	
Deelder, C. L.	1951	NNNR 59
Dixon, D. J. and C. J. Walters	1976	
Doan, K. H.	1942	
Dryer, W. R. and J. Beil	1968	
Dryer, W. R. and G. R. King	1968	
Dunson, W. A. and R. R. Martin	1973 X	
Durbin, A. G., S. W. Nixon and C. A. Oviatt	1979	
Dymond, J. R.	1944 X	
Ebel, W. J.	1970 X	
Ebert, C. H.	1978	
Eck, Gary W. and LaRue Wells	1983	
Edmondson, W. T.	1961 X	
Egglisshaw, H. J. and P. E. Shackley	1980 X	
El-Zarka, S.	1959	
Elrod, J. H.	1974	
Elrod, O'Gorman, Bergstedt, and Schneider	1980	CSYN
Elser, Allen A.	1968	
Etsey, C. A. and R. T. Thomson	1977	
Elson, P. F.	1967	

Elton, C.	1927	X
Elton, Charles S.	1958	X
Elwood, Jerry W. and Thomas F. Waters	1969	CSNR 12
Embody, G. C.	1934	X
Endeon, R.	1976	X
Eschmeyer, R. W.	1936	
Eschmeyer, R. W.	1937	
Eschmeyer, R. W.	1942	X
Eschmeyer, P. H.	1957	NSNR 27
Eschmeyer, Paul H., ed.	1975	
Eshenroder, R. L.	1977	CNYR 62
Fagan, J. A. and L. C. Fitzpatrick	1978	X
Finucane, J. H.	1965	X
Foerster, J. W. and S. P. Reagan	1977	
Forester, Timothy S. and J. M. Lawrence	1978	
Forney, J. L.	1961	X
Forney, J. L.	1965	
Forney, J. L.	1966	X
Forney, John L.	1967	
Forney, J. L.	1971	
Forney, John L.	1974	
Forney, J. L.	1975	
Forney, J. L.	1976	
Forney, J. L.	1977	
Forney, J. L.	1983	
Fortier, L. and W. C. Leggett	1970	X
Fox, W. W. Jr.	1979	
Francis, G. R., J. J. Magnuson, H. A. Regier, D. R. Taihelm	1979	
Frank, Kenneth T. and William C. Leggett	1982	
Frank, Kenneth T. and William C. Leggett	1983	
Fraser, J. M.	1978	CSYR 53
French, Donald P.	1980	
Frey, D. G.	1955	
Freyre, Lauce	1973	
Frost, W. E.	1945	X
Frost, W. E.	1954	
Frost, W. E. and C. Kipling	1967	
Frost, W. E. and C. Kipling	1980	X
Fujita, H. and S. Utida	1953	X
Fukuda, Y.	1962	X CNNN
Gaboury, M. N. and J. W. Patalos	1984	
Gadgil, M. and W. H. Bossert	1970	
Gannon	1971	
Gangmark, H. A. and R. D. Broad	1955	X
Gard, Richard and Donald W. Seegrift	1972	
Gasaway, C. R.	1970	
Gause, G. F.	1934	X
George, C. J. and J. H. Gordon II.	1976	X
George, T. T.	1982	---
Gerdes, J. H. and Wm. J. McConnell	1963	X
Gerking, Shelby D.	1966	
Gerking, S. D. ed.	1967	
Gerking, S. D.	1976	

Gill, D. E.	1978	X
Golden, M. F. and C. E. Twilley	1976	
Goodyear, C. P.	1977	
Goodyear, C. Phillip	1979	C--N
Goodyear, C. P.	1980	C--N
Graham, J. J.	1956	
Great Lakes Fish Lab.	1970	
Greenbank, J.	1945	X
Grice, F.	1957	
Grice, F.	1959	CSYR 54
Gulland	1977	
Gunning, Gerald E. and Tim M. Berra	1968	CSNR 16
Gunther, G.	1941	X NSNN
Gunther, Gordon	1947	
Gunter G. and H. H. Hildebrand	1951	X
Haines, Terry A.	1973	
Haldane, J. B. S.	1953	X
Haley, R., S. P. Davis, and J. M. Hyde	1967	X
Hallam, J. C.	1959	X
Hall, D. J., W. E. Cooper, and E. E. Werner	1970	
Hansen, D. J.	1970	
Hansen, M. J. and T. M. Stauffer	1971	X
Hanson, D. L. and T. F. Waters	1974	CSYR 15
Harrell, H. L.	1978	
Hartman, W. L.	1972	
Hartman, W. L.	1973	
Harvey, H. H. and S. B. Smith	1961	X
Harvey, H. H.	1975	
Hashagen, K. A. Jr.	1973	
Hasler, Arthur D.	1947	
Haslouer, Stephen G.	1979	X
Hausen, D. J.	1970	X
Haven, D. S.	1957	
Havey, Keith A.	1961	
Havey, Keith A.	1973	
Hayes, F. R. and D. A. Livingstone	1955	
Hazel, C.	1976	X
Healey, M. C.	1975	CNVR 10
Healey	1978	
Healey, M. C.	1980	CSYR 9
Hedtko, S. F. and F. A. Puglisi	1980	X NNNN
Heinle, D. R. and coauthors	1974	X NNNN
Henderson, Collins, and Reckahn	1983	
Henry, F. D., Jr.	1979	X
Hergenrader, G. L. and Q. P. Bliss	1971	
Herrington, W. C.	1944	
Herrington, W. C.	1947	X
Hesse, Wallace, and Lehman	1976	
Hewson, L. C.	1959	X
Hida, T. S. and D. A. Thomson	1962	X
Higley, D. L. and C. E. Bond	1973	CSYR 32
Hile, R. and H. J. Deason	1934	X

Hile, R.	1936	
Hile, R.	1937	X
Hile, R. and F. W. Jobes	1941	X
Hile, Ralph	1950	
Hile, R., P. H. Eschmeyer, and G. F. Langer	1951	
Hile, R., G. F. Lunder and H. J. Buettner	1953	
Hile, R.	1954	
Ho, C. L. and H. Karim	1978	X
Hoffmann, C. H. and A. T. Drooz	1953	
Holden, A. V.	1973	37
Holgate, P.	1967	
Holling, C. S.	1973	CSNR 11
Holling, C. S. (ed.)	1978	
Hood, D. W. (ed.)	1971	X
Hoopes, R. L.	1975	X
Horne, Alexander J., P. Javornicky, and C. R. Goldman	1971	X
Houde, E. D.	1967	
Houser, A. and J. E. Dunn	1967	NNNN
Hubbs, Carl L. and A. B. Rechnitzer	1952	X
Huish, M. T.	1957	
Huish, M. T. and G. B. Pardue	1978	X
Hulsey, Andrew H.	1956	
Huntsman, A. G.	1942	X
Hunter, J. G.	1959	
Hurley, D. A. and W. J. Christie	1977	
Idyll, C. P.	1973	
Istock, C. A.	1967	
Jackson, C. H. N.	1939	
Jackson, S. W. Jr.	1957	
Jackson, P. N. B. and K. H. Rogers	1976	
Jenkins, R. M.	1955	
Jenkins, R. M.	1957	
Jensen, A. L.	1971	
Jensen, A. L.	1981	CNNR 43
Jester, D. B.	1971	
Jester and Jensen	1972	
Jilek, R., B. Cossell, D. Peace, Y. Garza, L. Riley, and J. Stewart	1979	X
Jobes, F. W.	1952	
John, K. R. and A. D. Hasler	1956	
John, K. R.	1964	
Johnson, W. E.	1965	
Johnson, J. E.	1970	
Johnson, J. E.	1971	
Johnston, D. A.	1977	X CNNN
Johnson, F. H.	1977	CSYR 19
Johnston, C. E. and J. C. Cheverie	1980	NSNR 17
Johnson, L.	1983	
Jones, R.	1973	
Jones, D.	1975	
Jones, D. D. and C. J. Walters	1976	NSNR 44
Jones, D. D.	1977	
June, F. C.	1974	X

June, F. C.	1976	
Kanciruk, Paul, James E. Breck, Douglas S. Vaughan	1982	
Katz, Max and A. R. Gaufin	1952	
Kelener, J. J.	1972	NNNR 23
Kelso, J. R. M. and F. J. Ward.	1972	X
Kelso, J. R. M., T. B. Bagenal	1977	NNNR 55
Kelso, J. R. M. and F. J. Ward.	1977	X
Kempinger, J. J., and W. S. Churchill.	1972	X
Kempinger, J. J., W. S. Churchill, G. R. Priegel, L. M. Christenson	1975	
Kempinger, James J. and R. F. Carline	1977	
Kennedy, W. A.	1953	X
Kennedy, W. A.	1954	X
Kennedy, Harry D.	1955	
Kenyon, R. B.	1978	CSYR 42
Kerr, S. R. and R. A. Ryder	1977	
Kerswill, C. J.	1967	
Kerswill, C. J. and H. E. Edwards	1967	
Kesteven, G. L.	1947	
Kilambi, R. V. and R. E. Baglin Jr.	1969	
Kilambi, R. V.	1980	X
Kilgen, Ronald H.	1978	
Kimsey, J. B.	1954	X
Kipling, C. and W. E. Frost	1970	
Kipling, C.	1983a	
Kipling, C.	1983b	
Kneib, R. T.	1981	CNYR 4
Knittel, M. D., G. A. Chapman, and R. R. Garton	1980	X
Knudsen, E. E. and W. H. Herke.	1978	CSYN
Kohler, C. C.	1980	
Kohler, C. C. and J. J. Ney	1980	CSYR 22
Kohler, Christopher C. and John J. Ney	1981	CSYN
Kramer, D. and P. E. Smith.	1971	
Krovina, V. M.	1961	X
Krumholz, Louis A. and W. L. Minckley	1964	
Krykhtin, M. L.	1972	C--N
Kushian, James A.	1974	NSNR 30
Kushian, J. A.	1980	
Laarman, P. W.	1969	
Lackey, Robert T.	1970	
Lagler and Applegate.	1942	
Lagler, K. F. and H. Van Meter.	1951	X
Lambou, V. W.	1965	
Langford, R. R. and W. R. Martin.	1940	X
Langlois, Thomas H.	1941	
Langford, R. R.	1949	
Langford, T. E.	1983	CSNN
Larimore, R. W. Gilders, and C. Heckrotte	1959	
Larkin, P. A. and S. B. Smith.	1954	
Lark, D.	1954	
Larkin, P. A.	1963	
Larkin, P. A. and W. E. Ricker.	1964	X
Lark, J. G.	1973	X

Larkin, P. A.	1977bX
Larkin, P. A.	1977a
Latta, W. C.	1962 X
Laurence, G. C., T. A. Halavic, et. al	1979
Lawler, G. H.	1965
Lawrie, A. H.	1970
Lawrie, A. H. and J. F. Rahrer	1972
Lawrie, A. H. and J. F. Rahrer	1973
LeCren, E. D.	1949 X
LeCren, E. D.	1951
LeCren, E. D.	1958
LeCren, E. D. and M. W. Holdgate(ed.)	1962 X
LeCren, E. D.	1962
LeCren, E. D.	1965
LeCren, E. D.	1972
LeCren, E. D.	1973
LeCren, E. D.	1977
Leach, J. H. and S. J. Nepszy	1976
Leach, J. H., M. G. Johnson, Kelso, J. Hartmann, W. Numann and Entz	1977
Leggett, W. C., K. T. Frank, and J. E. Carscadden.	1984
Lett, P. F. and A. C. Kohler	1976
Levins, R.	1968 X
Levins, R.	1978 X
Lewis, S. L.	1969 X
Li, U. W. and P. B. Moyle	1981 X
Libosvsky, J. and D. W. Saeed	1983 X
Likens, G. E., F. H. Bormann, N. M. Johnson, D. Fisher, R. Pierce	1970 X
Likens, G. E. and F. H. Herbert	1974 X
Lindstrom, T. and N.-A. Nilsson	1962
Linfeld, R. S. J.	1979 X
Livingston, R. J.	1975
Lockwood, S. J.	1980 X
Lotrich, V. A.	1973
Lowe, C. H. C. S. Hinds, and E. A. Halpern	1967 X
Lumby, J. R. and G. T. Atkinson	1929 X
Lusk, S.	1981
Mac Arthur, Robert and D. W. Ranch	1955 X
Mac Arthur, Robert	1955 X
MacCallum, W. R. and H. A. Regier	1970
Maclean, James and J. J. Magnuson	1977
Maclean, J. A., D. O. Evans, N. V. Martin, and R. L. Desjardine	1981 X
MacPhee, C. and M. A. Brusven	1976 X
Madson, Chris	1982 X
Madson, J. J. and D. J. Karlen	1970 X
Magnuson, John J.	1976
Magnuson, J. J., H. A. Regier, W. J. Christie, and W. C. Sozogni	1980
Mahon, R. and M. Ferguson	1981
Maitland, P. S.	1972
Maloney, J. E. and F. H. Johnson	1957 X
Mansueti, R. J.	1961
Mansueti, R. J.	1964
Marais, J. F. K.	1982 X
	CSYR
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Marcy, B. C. Jr.	1971	X
Marcy, B. C. Jr. and F. P. Richards	1974	
Margetts, A. R. and S. J. Holt	1948	
Martin, N. V. and F. E. J. Fry	1972	
Martin, N. V. and F. E. J. Fry	1973	
Marzolf, G. R.	1978	X
Matlock, G. C., R. A. Marcello Jr. and K. Strawn	1975	
Mattingly, Rosanna L. and Niles R. Kevern	1979	
Mc Cauley, Rita N.	1966	X
Mc Crimmon, H. R.	1968	X
Mc Caull, Julian	1969	X
McCammon, G. W. and C. Von Geldern Jr.	1979	
McConnell, W. T. and J. H. Gerdes	1964	
McFadden, J. T.	1961	
McFadden, J. J. and E. L. Cooper	1962	
McFadden, J. T. and E. L. Cooper	1964	
McFadden, J. T., E. L. Cooper and J. K. Anderson	1965	
McFadden, J. T., G. R. Alexander, and D. S. Shetter	1967	
McFadden, James T.	1977	
McGee, M. V., J. S. Griffith, and R. McLean	1977	
McLeod, L.	1953	
Meekin, T. K. and R. L. Allan	1974	
Meffe, G. K., D. A. Hendrickson, and J. N. Rinne	1982	X
Merna, James W.	1965	X
Messersmith, J. D.	1969	
Miller, E. M.	1940	X
Miller, R. B.	1947	
Miller, R. B.	1950	
Miller, R. R.	1957	
Miller, D. J. and R. S. Wolf	1958	X
Miller, R. R.	1960	
Miller	1960	
Minckley, W. S. and L. Krumholz	1960	
Moffett, J. W.	1957	
Momot, W. T., J. Erickson, and F. Stevenson	1977	
Montgomery, J. C., C. D. Becker	1980	X
Moody, H. L.	1957	
Moore, H. P.	1934	X
Moore, Richard H.	1976	X
Morgan, et al.	1978	X
Moring, J. R.	1981	
Mortensen, Erik	1977	
Mottley, C. M.	1940	
Moyle, J. B. and W. D. Clothier	1959	
Moyle, Peter B.	1976	
Mraz, D.	1968	X
Mullan	1958	
Murawski, S. A. and C. F. Cole	1978	
Murdoch, W. W.	1966	
Murphy, G. I.	1968	
Murphy, G. I.	1977	
Murray, B. G. Jr.	1979	

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NNNN
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		CNVR	56
Nakashima, Brian S. and W. C. Leggett	1975	
Nakatani, R. E.	1969	
Neave, F.	1953	
Nebecker, Alan V., G. R. Bouck, and D. G. Stevens	1976	X
Nebecker, Alan V., D. G. Stevens, and R. K. Stroud	1976	X
Nebecker, Alan V., D. G. Stevens, and R. J. Baker	1979	X
Nebecker, A. V., A. K. Hauck, F. D. Baker, and S. L. Weitz	1980	X
Neess, J. C., W. T. Helm, and W. Threinen.	1957	
Neill, William H. and J. J. Magnuson	1974	
Nelson, W. R.	1974	
Nelson, W. G. Horak, M. Lewis, and J. Colt	1976	X
Nelson, W. R. and C. H. Walburg.	1977	
Nepszy, S. J.	1977	
Ney, J. J. and L. L. Smith Jr.	1975	
Nicholls, K. H., W. Kennedy and C. Hammett	1980	X
Nickolson, A. J.	1933	X
Nickolson, A. J.	1954	
Nickolson, R. S., N. Reimers, and H. D. Kennedy	1957	X
Nigro, A. A.	1980	
Nikolshkii, G. V.	1969	X
Nikolsky, G. A., A. Bogdanov and Yu Lopin.	1973	
Noble, R. L.	1972	X
Norden, C. R.	1967	
Northcote, T. G.	1972	
Northcote, T. G.	1973	X
Odell, T. T.	1934	X
Odum, W. E.	1970	X
Oglesby, G. B., W. C. Noell, H. O. Delo, W. A. Dyer, and others	1978	X
Oliver, James L., P. L. Hudson, and J. P. Clugston	1977	X
Olmsted, Larry L. and Donald G. Cloutman	1974	
Otto, R. G., M. A. Kitchel, and J. O. Rice	1976	X
Paloumpis, A. A.	1958	
Paltoheimo, J. E.	1961	X
Paltoheimo, J. E. and A. C. Kohler.	1968	
Parsons, J. W. and J. B. Kimsey.	1954	
Parsons, J. W.	1966	
Parsons, J. W.	1970	
Parsons, J. W.	1971	
Parsons, J. D.	1976	
Paterson, Colin G. and W. R. Turner	1968	X
Patriarche, M.	1952	X
Patriarche, M. H. and R. S. Campbell	1957	
Paulik, G. J.	1971	
Pauly, D.	1980	
Pearce, William A.	1980	
Pedrin, O. and H. Shainberg.	1974	
Peterman, R. M.	1984	
Pfister, L. A. and J. R. Holt	1978	X
Phillips, J. B.	1949	X
Phillippy, C. L.	1964	
Pippy, J. H. C. and G. M. Hare.	1969	X
Pollard, H. A. II and T. C. Bjornn.	1973	

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Powers, E. B.	1938	X
Powers, E. B., A. R. Shields and M. E. Hickman	1939	X
Prevost, G.	1960	
Priegel, G. R.	1969	
Priegel, G. R.	1971	CSYR 49
Priegel, G. R.	1978	X
Pritchard, A. L.	1929	
Provine, W. C.	1976	
Pycha, R. L.	1961	X
Pycha, R. L. and G. R. King	1975	
Pycha, R. L.	1980	NNNN
Pycha, R. L.	1981	NNNN
Radovich, J.	1967	
Rahrer, J. F.	1978	NSNR 41
Raleigh, Robert F., D. H. Bennett, L. O. Mohn, and O. E. Maughan	1957	X
Rawson, D. S.	1979	
Raymond, Howard L.	1963a	
Regier, H. A.	1963b	
Regier, H. A.	1966	X
Regier, H. A. and D. S. Robson	1969	
Regier, H. A., V. C. Applegate and R. A. Ryder	1972	X
Regier, H. A. and K. H. Loftus	1973	
Regier, H. A.	1973	
Regier, H. A. and W. L. Hartman	1978	X
Regier, H. A.	1979	
Regier, H. A.	1979	
Renfro, William C.	1963	X
Rhodes, R. J. et. al.	1974	
Ricker, W. E. and J. Gottschalk	1940	NSNR 6
Ricker, W. E.	1946	
Ricker, W. E.	1947	X
Ricker, W. E. and R. E. Foerster	1948	
Ricker, W. E.	1952	
Ricker, W. E.	1954a	
Ricker, W. E.	1954b	
Ricker, W. E.	1958	X
Ricker, W. E.	1963	
Ricker	1977	
Robson, D. S. and D. G. Chapman	1961	X
Roelofs, Eugene W.	1957	
Roelofs, E. W.	1958	X
Roff, D. A.	1984	
Rose, E. T. and T. Moen	1952	CSYR 29
Rosenzweig, Michael L.	1971	X
Rosenthal, H. and D. F. Alderdice	1976	
Ross, S. T. and J. A. Baker	1983	NNYR 7
Rothschild, B. J.	1966	
Rounsefell, George A.	1975	X
Royal, L. A.	1953	X
Rucker, Robert R. and P. M. Kangas	1974	X
Rupp, R. S.	1959	
Rupp, Robert S. and Malcolm A. Redmond	1966	
Ryan, P. M. and H. H. Harvey	1980	CSYR 57

Ryder, R. A.	1968	X
Ryther, J. H.	1969	X
Saiki, M. K. and J. C. Tash	1978	X NNNN
Sakagawa, G. T. and R. L. Pycha	1971	
Sanders, Howard L.	1978	X
Saunders, J. W.	1969	
Saunders, L. H. and G. Power.	1970	
Saville, A. and D. Schnack	1981	
Schaefer, M. B.	1968	
Schaefer, M. B.	1970	
Schaaf, W. E. and G. R. Huntsman.	1972	
Schaffer, W. M.	1974	X
Schaffer, W. M. and P. F. Elson.	1975	
Schlusser, I. J.	1982	X NNNN
Schmitz, William R. and Roland E. Hetfeld	1965	
Schneberger, Edward	1935	X
Schneberger, E.	1937	X
Schneberger, Edw., ed.	1970	
Schneider, J. C.	1973	
Schneider, J. C.	1977	
Schneider, J. C. and J. H. Leach	1977	CNN
Schneider, James A.	1979	X
Schoffman, R. J.	1941	
Schofield, C. L.	1976	
Schuck, H. A.	1945	
Schupp, D. H. and V. Macins	1977	
Schubel, J. R. and B. C. Marcy	1978	
Scott, D. P.	1962	
Scott, W. B. and W. J. Christie	1963	
Seber, G. A. F.	1973	X
Seegrift, Donald W. and Richard Gard	1972	
Seepot, Ralph M.	1978	
Shelton, W. L., R. O. Smitherman, and G. L. Jensen	1981	X
Shepherd, J. G. and D. H. Cushing	1980	
Sheppard, C. R. C.	1982	X CNN
Sherl, A. N. and G. Power.	1968	
Shetter, D. S. and A. S. Hazzard.	1939	X
Shields, J. T.	1957	
Shireman, J. V., D. E. Colle, and M. J. Maceina	1980	X
Shuter, B. J. and J. F. Koonce.	1977	
Shuter, B. J., J. F. Koonce and H. A. Regier.	1979	
Shuter, B. J. and J. F. Koonce.	1979	
Siddiqui, A. Q.	1979	X NNNN
Siegler, H. R. and H. Pillsbury.	1949	X
Silliman, R. P.	1975	
Simco, B. A. and F. B. Cross.	1966	
Simpson, A. C.	1953	X
Smith, M. W.	1935	
Smith, L. L. Jr. and J. B. Moyle.	1945	X
Smith, M. W.	1948	
Smith, M. W.	1950	
Smith, L. L. Jr. and L. W. Krefting.	1954	

Smith, M. W.	1956	X	CNNN
Smith, L. L. Jr. and R. L. Pycha	1960	X	
Smith, S. H.	1960		
Smith, S. H.	1964		
Smith, S. H.	1968		
Smith, Stanford H.	1970		
Smith, H. A. Jr.	1972	X	
Smith, Stanford H.	1972		
Smith, L. L. Jr.	1977		
Smith, P. E.	1978		
Snyder, G. R.	1969		
Solomon, M. E.	1949		CNNN
Solomon, V. E. F.	1950	X	
Spangler, George R.	1970		
Spangler, G. R., N. R. Payne, J. E. Thorpe, and coauthors	1977		
Spangler, G. R. and J. J. Collins	1980		CNYR 8
Spratt, J. D.	1972		
Spratt, J. D.	1973		
Springer, S.	1957	X	
Sprugel, George, Jr.	1954		
St. Pierre, R. A. and J. Davis	1972		
St. Pierre, R. A. and W. J. Hoagman	1975		
Staggs, M. D.	1982		
Stanley, Jon G., W. W. Miley II, and D. L. Sutton	1978		
Stearns, S. C.	1980	X	
Stegemon, John J.	1978	X	
Stenson, J. A. E., J. Bohlin, et. al.	1978		
Stevenson, J. C.	1944	X	
Stewart, Kitchell, and Crowder	1981		CSYN
Stober, Q. J. and C. H. Hanson	1974		
Stober, Q. J., R. W. Tyler, C. F. Cowman, Jr., J. Wilcock, Quinnell	1979	X	NNNN
Stone, U. B.	1938	X	
Storey, M.	1937	X	
Stroud, Richard H.	1949b		
Stroud, R. H.	1949a		C--N
Sunada, J. S.	1975		
Swanson, B. L. and D. V. Swedberg	1980		CS-N
Swedburg, D. V.	1965		
Swedburg, D. V. and C. H. Walburg	1970		NNNR 48
Sweetman, H. L. and H. E. Warfel	1936	X	
Sweeney, Robert, R. Foley, C. Merckel, and R. Wyeth	1975	X	
Swenson, W. A. and L. L. Smith Jr.	1976		
Swingle, H. S.	1949		
Swingle, H. S.	1951		
Sztramko, L. K. and J. R. Paine	1984		
Talhelm, Daniel R. and Richard C. Bishop	1980		
Tanner, J. T.	1966	X	CNNN
Tarby, Martin	1974		CNYR 58
Tekei, G. C. and A. J. Chamberlain	1978	X	
Tharratt, R. C.	1959	X	
Tiemeier, D. W. and C. W. Deyoe	1968	X	
Tiffany, L. H.	1920		

Timmons, T. J., W. L. Shelton and W. D. Davies	1980	X	
Tompkins, W. A. and J. W. Mullan	1958		
Torblaa, R. L. and R. W. Westman	1980	CSYR	20
Tramer, Elliot J.	1977		
Tschaplinski, P. J. and G. F. Hartman	1983	X	NNNN
Turner, W. R.	1953		
Turnpenny, A. W. H. and R. Williams	1981	NSNR	21
Van Oosten, John	1937bx		
Van Oosten, J.	1937a		
Van Oosten, J. V.	1944		
Van Oosten, J.	1945		
Van Velson, R. C.	1974		
Van Winkle, Webster, ed.	1977		
Van Den Avyle, M. J. and B. J. Higginbotham	1979		
Vanicek, C. D.	1980	---	N
Vaughan, T. W.	1934		
Vaughan, Douglas S., Paul Kanciruk, and James E. Breck	1982		
Vaughan, D. S., R. M. Yoshiyama, J. E. Breck, and D. L. DeAngelis	1982		
Vrooman, A. M., P. A. Paloma, and J. R. Zweifel	1981	X	
Waggoner III, J. P. and C. R. Feldmeth	1971	X	
Wagner, W. C.	1972	X	
Wales, J. H.	1942	X	
Wales, J. H.	1948		
Walker, R. E. and R. L. Applegate	1976		
Wallace, D. H.	1941	X	
Walsh, John	1968	X	
Walters, C. J.	1975	X	
Walters, C. J. and R. Hilborn	1976	X	
Walters, Steer, and Spangler	1980	CSNR	45
Warner, K. and O. C. Fenderson	1962		
Warshaw, S. J.	1972		
Watt, K. E. F.	1968	X	
Weatherley, A. H. and H. S. Gill	1981	X	
Weier, J. LeRoy and Donald F. Starr	1950		
Weinstein	1983	X	NNNN
Weitkamp, D. E. and M. Katz	1980		
Welcome, Robin L.	1979	X	
Wells, LaRue and A. L. McLain	1972		
Wells, L. and A. L. McLain	1973	C--N	
Wells, L.	1977	CSYR	52
Wells	1980		
Westgard, R. L.	1964	X	
Whillans, T. H.	1977	X	NNNN
Whillans, T. H.	1979		
Whitney, A. N. and J. E. Bailey	1959		
Whitaker, J. O.	1975	X	
White, Alan W.	1977	X	
White, Alan W.	1980	X	
White, A. W.	1981b		
White, Alan W.	1981ax		
Wiborg	1976	NSNN	
Wickliff, E. L.	1953		

Wickett, W. P.	1954
Wiley, Robert and D. Dufek	1977
Wilson, E. O. and W. H. Bossert	1971 X
Winters, G. H.	1976
Wirth, T. L.	1958
Wolfert, D. R.	1969
Wolfert, D. R.	1977
Woodbury, L. A.	1941 X
Wood, R. and A. R. Strachan	1970
Woolcott, W. S.	1962 X
Wrenn, W. B.	1968
Wrenn, W. B.	1975 X
Wright, R. F.	1976
Wright, G. L. and G. W. Wightl	1980 C--N
Wydoski, R. S. and E. L. Cooper	1966 X
Youngs, William D. and R. T. Oglesby	1972
Zeeman, E. C.	1952
Zilliox, R. G. and W. D. Youngs	1958 X